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NGUYEN THAO NGUYEN

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KAPOSVÁR UNIVERSITY
FACULTY OF AGRICULTURAL AND ENVIRONMENTAL SCIENCES
Department of Animal Genetics and Biotechnology

Head of Doctoral School
Prof. Dr. MELINDA KOVÁCS
Correspondent Member of the Hungarian Academy of Sciences

Supervisors
Dr. habil. ISTVÁN NAGY
Senior researcher
Prof. Dr. INO CURIK
Full professor

ESTIMATION AND UTILISATION OF DOMINANCE EFFECTS IN RABBIT POPULATIONS

Written by
NGUYEN THAO NGUYEN

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2. Introduction

For several decades the basic goal in animal breeding has been to improve traits of economic interest. This goal is being accomplished by identifying the individuals having superior genetic merit then selecting these animals to create the next generation. This process is accomplished by means of the breeding program where prediction of breeding values (genetic evaluation) is one of the most important elements of the selection process.

Although the theoretical basics were developed 40 years ago (Henderson, 1975) breeding value prediction could not become widespread until the development of softwares from the 1990s (Boldman et al., 1993; Groeneveld, 1990; Meyer, 1989) that could be applied estimating the breeding values (based on pedigree and performance data). Since the early 1990s the breeding value prediction became wide spread worldwide in every domesticated species and selection has been based on the BLUP (best linear unbiased prediction) breeding values in cattle (Dempfle, 1977), pigs (Hudson et al., 1985), sheep (Olesen et al., 1995) and rabbit (Estany et al., 1989). In Hungary the method also became widespread. In cattle the breeding value estimation of the bulls was based on the BLUP sire models as early as 1985 then on the animal models from 1999 (Nagy et al., 2004). Compared to cattle the BLUP method was introduced a bit later in pigs (Groeneveld et al., 1996), sheep (Nagy et al. 1999) and in rabbits (Nagy et al., 2006).

The common feature of the above mentioned studies was that the genetic evaluation focused only on the additive genetic effects while ignoring non-additive genetic effects (dominance and epistasis). As noted by Norris et al. (2010) genetic evaluation in any livestock species has been for the prediction of transmitting ability which is due to additive genetic effects. Although non-additive genetic effects are not directly transmitted from parents to offspring, they are important for traits closely related to fitness or having low heritability (Falconer, 1989). In fact the significant contributions to phenotypic variation - especially fitness and reproductive traits - of the dominance genetic effects has also been observed in a number of studies (Norris et al., 2006). Estimating dominance variance has been a subject of interest for decades (Maki-Tanila 2007) as there are several reasons for estimating dominance variation: an unbiased estimation of variance components (Misztal 1997), more precise prediction of additive effects with the effects of gene interactions included in the genetic evaluations (Henderson, 1989; Misztal et al., 1996), and usage of dominance effects through a crossbreeding or planning of mating schedule.

Dominance influences all genetic parameters related to cross- breeding (Wei et al., 1991a; Wei et al., 1991b). Pigs and rabbits, as prolific multiparous species, within populations usually have a large number of non-additive relationships (i.e., full-sibs) (DeStefano and Hoeschele, 1992). Van Tassell et al. (2000) suggested that a minimum of 20% full sibs should be in the population for successful estimation of non-additive genetic variation. Information on non-additive genetic effects is limited. Culbertson et al. (1998) showed estimates of dominance to be 25 % and 78% of additive genetic variance for number born alive and 21 day litter weight, respectively in Yorkshire pigs. In a study related to pigs Norris et al. (2010) showed that estimates of additive genetic variance were 0.554, 16.84 and 4.535 for number born alive (NBA), interval between parities (FI) and 21-day litter weight (LWT21), respectively. Corresponding estimates of dominance variance were 0.246, 9.572 and 0.661, respectively. As also noted by Toro and Varona (2010), we need to remember that ignoring non-additive genetic effects will produce less accurate estimates of breeding values and will have an effect on rankings. Technically it is now also possible to consider dominance effects; however, mainly due to the technical and computational difficulties dominance effects are still usually ignored from animal models (Toro and Varona, 2010).

Scientific research connected to rabbit breeding has a long tradition at the Kaposvár University. Since 1988 scientific staff of Kaposvár University has developed 3 different rabbit breeds (Pannon White, Pannon Ka and Pannon Large) where two of these breeds have been selected for thigh muscle volume based on in vivo Computer Tomography measurements. This type of selection is unique worldwide and its efficiency was proved from different perspectives (Nagy et al., 2006; Szendrő et al., 2010; Szendrő et al., 2012). Besides, Pannon White rabbit breed also has an extremely long and complete pedigree which makes it highly suitable for analysing population structure and inbreeding depression (Nagy et al., 2010; Nagy et al., 2013a). In the classical approach based on the pedigree, confounding is a serious problem as it is not possible to separate dominance effects from the full-sib common environment. Utilisation of the abundant multi-generation data allows separation of dominance from non-genetic effects (Lee et al. 2010). In recent years the estimation of the dominance variance component has been analysed for reproductive traits in Pannon White (Nagy et al., 2013b) and Pannon Ka (Nagy et al., 2014) rabbit breeds based on family effects (extended animal model).

It should be concerned to face with the difficulties when introducing the dominance effect into the models that we should choose the appropriate structure of these models before

applied dominance effect into the models. Since the first evaluation genetic variances of rabbits' reproductive performance based on the Best Linear Unbiased Prediction (BLUP) (Estany, 1989), several similar studies have been published (Rastogi, 2000; García and Baselga, 2002a, Piles et al., 2006; Nagy, 2011a; Nagy, 2011b; Ragab, 2011) covering the most important breeds and hybrid breeds. Nevertheless, when analysing model structures applied by these authors, besides the obvious random effects (animal and permanent environmental effects) it can be seen that the considered factors of these studies are highly heterogeneous (mating buck, physiological status, kindling month, kindling season, inbreeding coefficient of the dam, etc.). Only few studies presented model comparisons (Piles et al., 2006; Nagy et al., 2011b), where repeatability and multi-trait models were compared. In most studies no extensive information was given to specify how the authors developed the structure of the model evaluating reproductive performance. Another important issue of genetic evaluation is to determine which genetic effects should be considered. In animal breeding mostly simplified models are applied, taking into account only the additive genetic effects. On the other side, other genetic factors can also influence inheritance of quantitative traits and consequently they have impact on the estimation of basic genetic parameters. The mitochondrial genome (mitogenome) is a closed circular DNA molecule, in rabbits the length of the molecule is approximately 17,245 nt varying by repeated motifs placed in the control region, that encodes for the synthesis of 13 proteins that are essential for the oxidative phosphorylation (OXPHOS) system and are responsible for the regulation of cellular energy metabolism (Wallace, 1999). Mitogenome is inherited only through the maternal lineage (Giles et al., 1980), thus, providing genetic mechanism for cytoplasmic inheritance with potential impact on the quantitative traits and the estimation of genetic parameters important in animal breeding (VanVleck, 2000 -chapter 19). Thus, in a simulation study, Boettcher et al (1996c) noted that ignoring cytoplasmic effects will lead to biased estimates of heritability. Starting with the study of Bell et al. (1985) cytoplasmic effects, analysed as effects of maternal lineages, were most comprehensively analysed in cattle populations on milk production (Kennedy 1986; Boettcher et al., 1996b; Boettcher et al., 1997) as well as on the growth traits (Pun et al., 2012). The similar models were also performed in poultry (Szwaczkowski et al., 1999), sheep (Hanford et al., 2003; Snowder et al., 2004). The estimated effects in all those studies varied from negligible to the impact of up to 5% of phenotypic variation (Gibson et al., 1997). However, in all those studies cytoplasmic effects were analysed under assumption that maternal lineages derived from the pedigree reflect mitogenome polymorphism. However, this is quite a relaxed assumption and to obtain more

accurate estimates cytoplasmic quantitative genetic models have to be further extended to the association analyses of the mitogenome polymorphism, from D-loop mtDNA to complete mitogenome, with production traits. Good examples are provided in studies related to cattle (Boettcher et al., 1996a), poultry (Li et al., 1998; Zhao et al., 2015), pig (Yen et al., 2007; Fernandez et al., 2008; Yu et al., 2015, Tsai et al., 2016), sheep (Chen et al., 2017) populations as well as to humans (Ruiz-Pesini *et al.*, 2000; Liu *et al.*, 2012) where association of certain mitogenome polymorphisms with quantitative traits have been analysed. Unfortunately, as far as we are aware, no single analysis has evaluated the impact of cytoplasmic effects, neither of maternal lineages nor of mitogenome sequence variation, on any of traits that are important in rabbit production. Thus, estimate the genetic parameters, predict the breeding values and effects of cytoplasmic and mitochondrial inheritance for litter size components of Pannon rabbits using several animal models (based on the available environmental factors) are applied in order to detect the structures of the "best" models.

3. Literature review

Dominance variance is one of the main features whose properties determine genetic variance. Genetic evaluation in commercial programs nowadays is widely based on BLUP, ensuring unbiased estimates if the full relationship matrix and all data used in selection are included in the evaluation (Blasco and Toro, 2014). Selection efficiency also depends on the magnitude of the non-additive variances. An intensive research is now being developed in this area. However, including non-additive effects like dominance effect in the applied models produces further complications. Thus, understanding the basis of dominance effect plays a vital role in the genetic improvement of farm animals.

3.1 A brief history

The concept of dominance, originally formulated by Gregor Mendel (Bennett, 1965) is fundamental to genetics. Though Mendel, "The Father of Genetics", first used the term in the 1860s, it was not widely known until the early twentieth century. Firstly, Fisher (1928) explained the overwhelming majority of deleterious mutations in the observed partial or complete dominance of wild-type alleles. However, based on physiological caused dominance effect was mentioned by Wright (1929, 1934). The theoretical models and empirical experiments suggest that substantial selection for dominance modifiers exists during the spread of adaptive alleles (Bourguet, 1999). According to Schlager (1974), genetic analysis yielded significant additive and dominance components in the inheritance of systolic blood pressure in mice. The estimates of non-additive components were highly variable but generally small compared to the additive genetic estimates in chicken populations (Silva et al., 1976). Genetic variance estimated from twin data into additive and dominance variances was presented using Falconer's variance component model, which seems to be the least affected by fluctuations in the magnitudes of dominance and environmental variances (Kang et al., 1977). Dominance components were two to four times the magnitude of additive components for dairy characters (Thomas et al., 1985). Mixed models including additive and non-additive genetic effects have been developed (Henderson, 1989; Meyer, 1989; Hoeschele and Van Raden, 1991). Egg production is also influenced by dominance (Fairfull and Gowe, 1990). Dominance influences all genetic parameters related to cross-breeding (Wei et al., 1991a; Wei et al., 1991b). Van Raden (1989), Hoeschele (1991), and Tempelman and Burnside (1991) have reported such estimation of dominance variance for dairy cattle traits. The results on dominance were in good agreement with heterosis and inbreeding depression for these egg production traits and it was described by Ming et al. (1993). Varona et al. (1999) found that the largest changes after adding the dominance effect to the model were for

animals with no own records and having many progenies by a single mate, e.g. dams of a single embryo-transfer batch in cattle. Non-additive genetic effects appear to be of sizeable magnitude for fertility traits and should be included in models intended for estimating additive genetic merit (Palucci et al., 2007). The use of the complete dominance relationship matrix may improve the estimation of additive genetic variances and breeding values in pigs (Dufrasne et al., 2014). Ignoring the dominance resulted in a slight overestimation of permanent environmental effects and these two effects showed partial confounding (Nagy et al., 2014).

3.2 Definition

Non-additive genetic variation results from interactions between genes and the most important non-additive genetic effects are those of dominance (Gengler et al., 1998). Dominance effects are caused by interactions of alleles at the same locus and are not directly transmitted from an animal to its progeny (Hoeschele and Van Raden, 1991). The prediction of additive and dominance genetic effects concurrently should allow for a more precise prediction of total genetic merit and breeding value and knowledge of the dominance effect may be beneficial for mate selection programs so that the genetic merit of the progeny can be maximized (Henderson, 1989). However, large populations are required to obtain acceptable accuracies for breeding values (Goddard and Hayes, 2009).

3.3 Genetic parameters

3.3.1 Cattle

The estimates of dominance effect and heritability for productive traits of cattle were generally different in magnitude and ranged from very low to moderate (Table 1). Allaire and Henderson (1965) presented the computed estimates of the dominance effects and heritabilities for first lactation records of milk and fat yields. With advances in the development of effective algorithms for large data sets, Tempelman and Burnside (1990, 1991) and Lawlor (1992) reported considerable dominance effects for the same traits in Holstein Friesian population.

Table 1. Additive and dominance components of productive traits in cattle

No.	References	Breed	Data size	Productive traits	Dominance effect	Heritability
1	Allaire et al., 1965	Holsteins	12,631	Milk yield	0.16	0.24
				Fat yield	0.24	0.23
2	Tempelman et al., 1990	Holsteins	60,892	Milk yield	0.06	0.40
				Fat yield	0.24	0.32
3	Tempelman et al., 1991	Holsteins	24,695	Milk yield	0.19	0.39
				Fat yield	0.34	0.43
4	Lawlor et al., 1992	Holsteins	55,641	Milk yield	0.12	0.32
5	Fuerst et al., 1994	SIM_PB_CB	375,093	MY1	0.08	0.18
		SIM_PB	322,166		0.09	0.20
		BVx BS	170,465		0.06	0.15
		SIM_PB_CB	254,441	MY2	0.07	0.15
		SIM_PB	217,310		0.07	0.16
		BVx BS	120,754		0.11	0.13
		SIM_PB_CB	168,744	MY3	0.05	0.17
		SIM_PB	143,865		0.04	0.18
		BVx BS	80,825		0.03	0.18
		SIM_PB_CB	208,857	LPL	0.21	0.13
		SIM_PB	198,483		0.19	0.13
		BVx BS	116,432		0.35	0.13
		SIM_PB_CB	208,857	LFCM	0.26	0.18
		SIM_PB	198,483		0.25	0.19
		BVx BS	116,432		0.52	0.13
6	Miglior et al., 1995	Holsteins	176916	LSCS	0.01	0.17

(5) SIM_PB_CB = Simmental including crossbreds, SIM_PB = pure bred Simnmental, and BV x BS = population of Braunvieh and crossbreds of Braunvieh with Brown Swiss; MY1 = milk yield of lactation 1, MY2 = milk yield of lactation 2, MY3 = milk yield of lactation 3; LPL= length of productive life, and LFCM = lifetime production of fat corrected milk; (6) LSCS = lactation mean of somatic cell score for first lactation.

The lowest dominance and highest heritability values were found in the study which was based on the biggest dataset (Tempelman and Burnside, 1990). Thus, these significant differences can mainly due to substantial improvement in the available hardware and software allowing the estimation of non-additive genetic variances from large files of field data (Fuerst and Sölkner, 1994).

For lactation traits, levels of dominance were quite constant through the tested breeds, except for the BV x BS data for second lactation, in which dominance was very high. Dominance and heritability estimates were highest (Table 1) in the first lactation among three lactations; estimating the second lactation were equal to or lower than that for third lactation and heritability decreased from first to third lactations (Strandberg, 1991).

Fuerst and Sölkner (1994) reported that dominance variance was important for most lifetime performance traits dominance was definitely higher than additive variance. Particularly, dominance variance was high for both traits and for all breeds especially for the population of Braunvieh and crossbreds of Braunvieh with Brown Swiss (BV x BS) data. Heritability

estimates for LPL was unchanged over all breeds (Table 1). Estimates for LFCM for BV x BS were outside of parameter limits because of high standard errors (0.06-0.1) and possible correlations between the genetic variances (Van Raden et al., 1992). McAllister et al., 1990 found significant heterosis for most lifetime performance traits in a crossbred population of Holsteins. Heritability estimated by Miglior et al., (1995) for lactational measures of somatic cell score for first lactation was almost twice as large as the dominance component, but, overall, non-additive genetic variance was low.

Table 2. Additive and dominance components of reproductive trait in cattle

No.	References	Breed	Data size	Reproductive trait	Dominance effect	Heritability
1	Hoeschele et al., 1991	Holsteins	379,009	DO	0.02	0.02
				DO150	0.01	0.02
				SP	0.01	0.01
				SP91	0.03	0.01
2	Hoeschele, 1991	Holsteins	379,009	DO	0.02	0.02
				AI period	0.01	0.01
3	DeStefano et al., 1992	Cows	400	Mating strategy 1	0.05	0.05
				Mating strategy 2	0.10	0.15
				Mating strategy 3	0.15	0.25
4	Fuerst et al., 1994	Simmental	304,493	CI 1	0.04	0.02
			191,772	CI 2	0.02	0.02
			126,969	CI 3	0.00	0.03
5	Fuerst et al., 1994	SI(al1)	354,247	CI1	0.04	0.02
		SI (pure)	304,493		0.04	0.02
		BVx BS	148,105		0.01	0.01
		SI(al1)	224,130	CI2	0.02	0.01
		SI (pure)	191,772		0.02	0.02
		BVx BS	99,973		0.00	0.02
		SI(al1)	149,017	CI3	0.00	0.03
		SI (pure)	126,969		0.00	0.03
		BVx BS	66,740		0.00	0.01
6	Van Raden et al., 2006	Cows	1,739,055	Embryo loss	0.03	0.01
7	Palucci et al., 2007	Cattle	486,012(heifers)	AFS	0.14-0.18	0.10-0.21
			507,315(cows)	NRR (heifers)	0.01- 0.02	0.01
				CTFS	0.06-0.07	0.10-0.11
				NRR (cows)	0.01	0.01

DO = Days open, DO150 = days open with an upper bound of 150 d, SP = service period (days between first and last insemination), SP91 = service period with an upper bound of 91day, AI = artificial insemination, CI 1 = Calving interval for lactations 1, CI 2= Calving interval for lactations 2, CI 3 = Calving interval for lactations 3; SI (all) =Simmental including crossbreds, SI (pure) =pure bred Simmental, and BV x BS = population of Braunvieh and crossbreds of Braunvieh with Brown Swiss; AFS = age at first service; NRR = non-return-rate; CTFS = interval from calving to first service

Accurate estimation of dominance variances is difficult because proportions of variance shared by relatives maybe small and confounded with other genetic or environmental effects

(Fuerst and Sölkner, 1994). Inclusion of dominance effects in genetic evaluation models can improve estimation of additive effects and should be considered in breeding programs.

The results of several studies examining fertility traits are presented in Table 2. Dominance variance was equal or larger than heritability for artificial insemination, days open (DO), service period (days between first and last insemination-SP) and service period with an upper bound of 91 days traits (SP91), excepting days open with an upper bound of 150 days trait (DO150) but dominance variance relied clearly on upper bounds. Dominance effect was negligible for DO and DO150, SP and SP91 although its value increased to double with upper bound days (Table 2). Heritability was equal levels for days open, service period and artificial insemination traits (Table 2). Alteration in female reproduction is owing to variations among cow in ability to conceive and that of the embryo to survive. Genetic variation in ability to conceive and in embryonic survival may have been reduced because all cows were fertile as heifers and were successful conceptions themselves (Hoeschele, 1991).

Turning to examine three mating strategies were shown by DeStefano and Hoeschele (1992) such as mating strategy 1 allocated sires to cows based on predicted specific combining ability (PSCA) among service sires and sires of the cows such that average PSCA was maximized by linear programming, mating strategy 2 were ranked by sire x maternal grandsires (MGS) combination effect and chosen sequentially sequential allocation by specific combining ability (SEQ) and mating strategy 3 were the average PSCA calculated for each MGS over all 10 service sires, to simulate the increase in progeny performance, heritability and the ratio of dominance to phenotypic variance, both showed increasing trend from the first mating strategy to the third one relied on predicted specific combining abilities among sires and maternal grandsires through random mating to avoid inbreeding that do not use specific combining ability. Fuerst and Sölkner (1994) reported about six inbred breeds of Holsteins and their reciprocal crosses, the results for calving interval about estimates of heritability computed in the present studies were in agreement with others at three lactation periods. Except for the population of Braunvieh and crossbreds of Braunvieh with Brown Swiss (BV x BS), dominance effect was equal or larger than do heritability and interestingly, equals to zero in term of calving interval 3. Comparison of the three period of lactation, heritability estimates did not decrease except for BV x BS in the third period. However, it has to be noted that, the magnitude of heritability and dominance estimates were all close to zero. Beckett et al. (1979) concluded that specific gene combinations and the way in which they were assembled can have an important influence on reproductive performance. Non-return

rate (NR) at day 70 after first insemination was evaluated as a trait of the embryo loss, which is caused by lethal recessive genes. Heritability estimates for this trait is substantially smaller compared to dominance variance. Dominance genetic variances were greater than heritability for age to first service, heifer non return rate, and interval from calving to first service and found the agreement with the findings of Miglior et al., (1995). Table 2 showed the results of several models estimating several non-additive genetic variances including dominance (D), additive-by dominance (AD) and dominance-by-dominance (DD), together with the additive genetic variance (A) and the model including only additive genetic effect. Comparing genetic variance estimates between heifer and cow in non-return rate, non-additive genetic variance estimates were similar in value. On the contrary the additive component was much greater for cows than for heifers. The possible reason may be that non-return rate in cows is influenced by other factors that regulate ovarian activity and may have a heritability value greater than that of non-return rate (Palucci et al., 2007). Heritability in the narrow sense (i.e. additive genetic variance to phenotypic variance) was lower when accounting for dominance genetic variances than using an additive animal model. This phenomenon was reported by Palucci (2007) in Table 2. Whenever gene interactions are omitted from the model their variance gets split between the additive and the residual effect therefore determining the additive effect to be overestimated. The consequences of this study on genetic evaluations for fertility traits, and maybe other traits, are that the ratio of the variance explained by non-additive genetic effects to phenotypic variance appears larger than heritability in the narrow sense for age at first service, heifer non-return rate and calving to first service (Palucci et al., 2007). Ignoring dominance genetic variances may result in additive genetic effects to be overestimated and possibly biased, as seen by comparison of the results in Table 2 with numerous studies on this issue. Estimates of dominance variance and heritability together with their standard errors of the eighteen confirmative traits are given in Table 3. These results suggest that significant differences existed in the estimates of dominance genetic variance and heritability between Rhodes and McNay lines (Table 3). The range of estimates was from low to moderately high. Particularly, the highest estimates of dominance variance were for WW; therefore, this trait is expected to present the largest degree of heterosis (Willham, 1970). The lowest estimates of dominance variance were observed for BWT, BH, and WH for both lines. Estimates of dominance variance and heritability were generally higher at the Rhodes herd than at the McNay herd for BWT, BH, and WW (Tables 3).

Table 3. Additive and dominance components of confirmative traits in cattle

No.	References	Breed	Data size	confirmative traits	Dominance effect	Heritability	Note
1	Rodríguez et al., 1995	Rhodes	3,992	Birth weight	0.00-0.39	0.31-0.60	
				Birth hip height	0.14-0.53	0.39-0.52	
				205-day weight	0.00-0.56	0.14-0.44	
		McNay	2,877	Birth weight	0.00-0.3	0.39-0.63	
				Birth hip height	0.00-0.33	0.10-0.51	
				205-day weight	0.16-0.27	0.19-0.37	
2	Misztal et al., 1997	Holsteins	600,678	Stature	0.07±0.01	0.45±0.003	
				Strength	0.08±0.01	0.28±0.01	
				Body depth	0.10±0.01	0.35±0.003	
				Dairy form	0.05±0.001	0.24±0.004	
				Rump angle	0.03±0.01	0.35±0.01	
				Thurl width	0.03±0.01	0.25±0.002	
				Rear led set	0.04±0.01	0.19±0.002	
				Foot angle	0.02±0.01	0.12±0.01	
				Fore udder att	0.05±0.01	0.24±0.01	
				Udder height	0.04±0.01	0.23±0.004	
				Udder width	0.03±0.01	0.19±0.003	
				Udder cleft	0.03±0.01	0.18±0.003	
				Udder depth	0.04±0.01	0.30±0.003	
				Front teat	0.03±0.01	0.25±0.003	
3	Gengler et al., 1998	Limousin cattle	215,326	Postweaning gain	0.10±0.01	0.21±0.01	Original contemporary model
					0.18±0.02	0.02±0.01	Alternative contemporary model

These differences could be due to sampling variance only; more records were available at Rhodes and the inverses of the dominance relationship matrices were denser for the data subsets from this herd, which could have resulted in better estimates of the parameter (Rodríguez et al., 1995).

Estimates of dominance and additive variances were obtained for next 14 linear confirmative traits in Holsteins. These traits are scored on a unified scale of one to 50, and have a similar phenotypic standard deviation of about 6.0, thus simplifying comparisons among them (Thompson et al., 1983). No clear relationship was found between the estimates of dominance and heritability and, particularly, larger estimates of dominance variances were generally associated with higher additive variances, but that association was weak. (Misztal et al., 1997); Table 3 presents estimates of dominance and heritability variances for the 14 traits are expressed as ratio of the phenotypic variance with the standard deviations. All traits with

larger estimates of dominance were strength, body depth and dairy form traits. Estimate of dominance variance was highest level for body depth and lowest for foot angle (Table 3). For all traits, the dominance variance was, on average 10 times lower than the heritability. The estimates of the dominance variance are low for some traits but there is a substantial variability for their magnitude.

Another study based on Limousin cattle, estimates of dominance variances were higher than heritability expressed as percentage of the phenotypic variance (Table 3) based on alternative contemporary model. The high values may indicate that dominance effect is important for post-weaning gain trait. Results showed the advantage of an individual dominance approach based on sire-dam combinations; therefore, expected gains through the use of specific combination ability as a part of the mating selection criteria for growth might be high (Gengler et al., 1998). A potential candidate for such variation in PWG could be the performance differences between males and females. Some changes may happen in estimated breeding values obtained with or without dominance genetic effects in the models. This approach should be superior to using expected heterosis on a breed level in commercial selection because allele interaction is directly modelled on a sire-dam base independently from breed origin (Gengler et al., 1998). Use of specific combining ability as described by Henderson (1988) might permit the exploitation of the observed dominance variance in commercial situations, upgrading, or purebred populations.

3.3.2 Pigs and rabbits

Dominance and heritability measurements for reproductive traits of pig and rabbit are presented in Table 4. All variances are expressed as a ratio of the phenotypic variance. Estimates of dominance variance were moderate and lower than additive variance for NBA and LWT on pig. According to Norris et al. (2006), the proportion of phenotypic variance accounted for by dominance effects for farrowing interval was larger than the heritability of additive effects for this trait, indicating the importance of dominance effects on this trait, although according to the study of Norris et al. (2010), dominance variance were lower than additive variance. This could be due to the small data size and the standard errors were large for the observed estimates especially the dominance.

Table 4. Additive and dominance components of reproductive traits in pig and rabbit

No.	References	Breed	Data size	Traits	Dominance effect	Heritability	Model
1	Culbertson et al., 1998	Yorkshire pig	179,485	NBA	0.02 ± 0.007	0.09±0.01	
				LWT	0.06 ± 0.09	0.08±0.001	
2	Ishida et al., 2001	Pig	285	NP	0.20	0.11±0.14	
				NW	0.00	0.05±0.01	
3	Norris et al., 2006	Landrace pigs	26,223	NBA	0.07± 0.01	0.10 ± 0.01	
			21,335	LWT	0.02 ± 0.02	0.07 ± 0.01	
			16,370	FI	0.03 ± 0.02	0.02 ± 0.01	
4	Norris et al., 2010	Duroc Pig	10,703	NBA	0.04±0.02	0.09±0.02	
			6,883	LWT	0.02±0.01	0.10±0.02	
			6,881	FI	0.01±0.01	0.02±0.01	
5	Angkuraseranee, 2010	Duroc Pig	1,481	NBA	0.10	0.17	
			1,477	BW	0.16	0.17	
			1,422	NW	0.05	0.37	
			1,421	WW	0.15	0.15	
6	Nagy et al., 2013b	Pannon white	3,883	NBA	0.12±0.02	0.09±0.01	AD
					0.12±0.02	0.09±0.01	ADF
					0.05±0.02	0.06±0.01	ADPe
					0.05 ±0.02	0.06±0.01	ADPeF
				NBD	0.06 ±0.02	0.02±0.01	AD
					0.06±0.02	0.02±0.01	ADF
					0.06±0.02	0.02 ±0.01	ADPe
					0.05±0.02	0.02±0.01	ADPeF
				TNB	0.15 ±0.03	0.10 ±0.01	AD
					0.15±0.03	0.10 ±0.01	ADF
					0.08 ±0.032	0.06 ±0.01	ADPe
					0.08 ±0.03	0.06 ±0.01	ADPeF
7	Nagy et al., 2014	Pannon Ka	11,582	NBA	0.05±0.01	0.10±0.02	single-trait
				NBD	0.04±0.01	0.07±0.01	
				TNB	0.12±0.02	0.02±0.01	
				NBA	0.05 ±0.01	0.09±0.02	two-trait
				NBD	0.07 ±0.01	0.03±0.01	

NBA = number born alive, LWT = 21-d litter weight, NP= the number of piglet born in total, NW = number weaned, FI = interval between parities, BW = birth weight; WW = weaning weight, NBD = number of kits born dead; TNB = total number of kits born, AD = model with additive and dominance effects; ADPe = model with permanent environmental, additive, and dominance effects; ADF= model with additive, dominance, and inbreeding (doe and litter) effects; ADPeF = model with permanent environmental, additive, dominance, and inbreeding (doe and litter)

However, a simulation study by Norris et al. (2002) revealed that even when the data set is small, as long as the magnitude of the dominance genetic variance is large, dominance genetic variances can be estimated with relatively good accuracies. Estimating the additive and dominance genetic variances for birth weight (BW), number weaned (NW), and weaning weight (WW) substantial magnitudes were found. For the number of piglet born in total trait, the narrow-sense heritability was smaller than dominance in the minor level. These ratios of the variance because of dominance effects were also not statistically significant largely due to

the large standard errors. The results suggest that dominance genetic effects affect expression of the traits studied. Several authors (Hoeschele, 1991; Fuerst and Sölkner, 1994) indicated that non-additive genetic variance could be relatively important in fertility traits since these traits show low additive genetic variance.

The estimated variance components based on rabbit data is presented in Table 4. Additive, dominance, and permanent environmental variance components were estimated for the number of kits born alive, number of kits born death, and total number of kits born of a synthetic rabbit line (called Pannon Ka). Using the models without and with dominance components such as AD, model with additive and dominance effects; ADPe, model with permanent environmental, additive, and dominance effects; ADF, model with additive, dominance, and inbreeding (doe and litter) effects; ADPeF, model with permanent environmental, additive, dominance, and inbreeding (doe and litter) effects, heritability estimates were low for all traits (NBA, NBD and TNB). The examined traits were evaluated using single-trait and two-trait (number of kits born alive-dead) animal models containing all or part of the following effects: additive genetic effects, permanent environmental effects, dominance effects (Nagy et al., 2014). Results showed that the dominance components for number born alive (NBA), number of kits born dead (NBD) and total number of kits born (TNB) were smaller or larger than heritability and various levels among the different models with the dominance effects (Table 4). Ignoring the dominance resulted in a slight overestimation of permanent environmental effects and these two effects showed partial confounding (Nagy et al., 2013b). Accuracy of genetic evaluations could be increased when dominance genetic effects are considered in the model of evaluation (Misztal, 1997; Van Raden et al., 1992; Johansson et al., 1993). These findings justify including dominance effects in models of litter size traits in populations that reveal significant dominance relationships.

Studies analysing growth traits of pig presented in Table 5. Data on lifetime daily gain from two purebred lines A, B, and their reciprocal crosses C were used to estimate dominance variance and heritability. The ratio of parental dominance to phenotypic variance was moderate for lines A, B, and C. These ratios are very large, suggesting that the parental dominance variance may be inflated and may also contain other variances, including full-sib environmental variances and non-additive variances other than dominance (Lutaaya et al., 2001).

Table 5. Additive and dominance components of growth traits in pig

No.	References	Breed	Data size	Traits	Dominance effect	Heritability	Note
1	Lutaaya et al., 2001	Landrace	6,022	LDG	0.39	0.51	line A
			24,170		0.16	0.38	line B
			6,135		0.29	0.29	line C
2	Culbertson et al., 1998	Yorkshire	239,354	DAYS	0.103 ±0.015	0.33±0.04	
				BF	0.048±0.007	0.44±0.09	
3	Ishida et al., 2001	Landrace	1,528	BL	0.19	0.38±0.07	
				HG	0.16	0.16±0.06	
				CC	0.26	0.28±0.07	
				WH	0.28	0.32±0.08	
				CD	0.1	0.04±0.03	
				SW	0.03	0.21±0.05	
				CW	0.18	0.07±0.04	
				HW	0.39	0.18±0.08	
				HH	0.19	0.42±0.07	
				DG	0.9	0.09±0.41	
			567	BWS	0.00	0.05±0.07	
				CWT	0.00	0.12±0.08	
				CL	0.00	0.50±0.11	
				CWD	0.01	0.26±0.1	
				BLI	0.24	0.32±0.14	
				BLII	0.09	0.31±0.11	
				PS	0.13	0.09±0.09	
				PH	0.47	0.07±0.15	
				MLA	0.49	0.32±0.2	
				MLL	0.00	0.21±0.09	
				MLW	0.00	0.20±0.09	
				ABF	0.28	0.33±0.15	
				AGF	0.53	0.47±0.21	
				KFW	0.29	0.44±0.16	
				NVT	0.14	0.19±0.1	
4	Dufrasne et al., 2014	Piétrain × Landrace	22,197	Body weight	0.22 - 0.4	0.19 - 0.42	Model 2
					0.05 - 0.11	0.31 - 0.53	Model 3

LDG = lifetime daily gain; Days = days to 104.5 kg; BF = back fat at 104.5 kg; BL = body length; HG = Heart girth; CC = cannon circumference; WH = withers height; CD = chest depth; SW = shoulder width; CW = chest width; HW = hip width; HH = hip height; DG = average daily gain; BWS = body weight before slaughter; CWT = cold carcass weight; CL = carcass length; CWD = carcass width; BLI = black loin I; BLII = back loin II; PS = percentage of shoulder weight; PH = percentage of ham weight; MLA = M. longissimusthoracis area; MLL = M. longissimusthoracis length; MLW = M. longissimusthoracis weight; ABF = average back fat thickness; AGF = average M. gluteus medius back fat thickness; KFW = kidney fat weight; NVT = the number of Vertebrae thoracicae.

However, the dominance variation should be accounted for lifetime daily gain. Heritability estimates for purebred lines were different to those for the crossbred line. Estimates of heritability for purebred lines obtained were generally higher than dominance effect, whereas both genetic parameters have the same ratio in the crossbred line. Animals ranked best as purebred are not necessarily breeding the best crossbreds (Lutaaya et al., 2001). Estimates dominance variance and heritability were obtained for days to 104.5 kg (DAYS), and back fat

at 104.5 kg (BF). All variances are expressed as a ratio of the phenotypic variance. Estimates of dominance variance were small magnitude for DAYS and BF. Dominance variance for DAYS and BF were estimated to be less than the additive variance in the narrow sense. Although the dominance variance for DAYS would seem large, similar results were found for growth traits in beef cattle (Gengler et al., 1998). The results indicate that dominance effects may be important for reproductive and growth traits in swine. The amount of dominance variance varied among traits. It is not surprising because the variance depends largely on gene frequencies at loci concerned and changes during selection (Ishida et al., 2001). However, the degree of dominance variances for chest depth (CD), chest width (CW), hip width (HW), average daily gain (DG), percentage of shoulder weight (PS), percentage of ham weight (PH); M. longissimus thoracis area (MLA); average M. gluteus medius back fat thickness (AGF) are greatly higher than that of heritability. Dominance effects could not be detected body weight before slaughter (BWS), cold carcass weight (CWT), carcass length (CL), M. longissimusthoracis length (MLL), M. longissimusthoracis weight (MLW), although the number of the piglet born in total (NP) and body length (BL) were affected. It appears necessary to consider the dominance effects in genetic evaluation of the selected lines. Dufrasne et al., (2014), estimated the dominance variance for repeated live BW records in a crossbred population of pigs from 50 to 210 d of age. Three single-trait random regression animal models were used: Model 1 without parental subclass effect, Model 2 with parental subclasses considered unrelated, and Model 3 with the complete parental dominance relationship matrix. Dominance variance was computed as 4 times the estimated parental subclass variance. Results presented that dominance effects exist for growth traits are reasonably smaller than heritability. Therefore, genetic variability in the studied population remains quite large and could explain the large heritability estimates for this population (Dufrasne et al., 2014). Estimated heritability and dominance effect in model 2 appeared to be lower compared with Model 3. Results of this study also showed that dominance variance exists for pig growth traits and that inclusion of dominance effects in genetic evaluation models is possible and will improve estimation of additive breeding values.

3.3.3 Poultry and fish

Table 6. Additive and dominance components of growth traits in poultry and fish

No.	References	Animal	Data size	Traits	Dominance effect	Heritability	Note
1	Rye et al., 1998	Salmon	58,920	Body weight	0.09	0.07	
			62,161		0.05	0.06	
			55,251		0.02	0.13	
			51,969		0.03	0.05	
2	Mielenz et al.,, 2006	Quails	7,934	BW42f	0.46±0.05	0.33±0.03	Line 1
				BW200f	0.09±0.04	0.38±0.03	
				BW42m	0.44±0.05	0.50±0.03	
				BW200m	0.21±0.08	0.49±0.04	
			7,214	BW42f	0.35±0.05	0.38±0.03	Line 2
				BW200f	0.10±0.02	0.38±0.04	
				BW42m	0.28±0.04	0.55±0.03	
				BW200m	0.23±0.08	0.52±0.04	
3	Gallardo et al., 2010	Salmon	11,833	Harvest weight	0.19	0.21	Even population
			10,327		0.06	0.37	Odd population

BW42f = the body weight of 42-day-old females; BW200f = body weight at an age of 200 days females; BW42m = the body weight of 42-day-old males; BW200m = body weight at an age of 200 days males

Dominance genetic variance and heritability estimates for growth traits of poultry and fish are summarized in Table 6. These traits were examined in numerous studies. Dominance genetic variance was smaller than additive genetic variance, except one population of 58,920 records where dominance variance was larger than additive genetic variance. The magnitude of dominance genetic variance and their effected the estimates of heritability found in this study encouraged significantly that dominance genetic variance should be considered in genetic evaluations for growth traits in salmon. Furthermore, estimates of heritability from models ignoring non-additive genetic effects were strongly biased upwards, illustrating a significant confounding between additive and non-additive genetic effects (Rye et al., 1998). Substantial reduction in the heritability estimates by including dominance effects in the model was previously reported for egg production traits in poultry (Wei et al.,, 1993). Ignoring non-additive genetic effects will likely have greater undesirable consequences in salmon than in cattle, as salmon populations have a higher level of average non-additive genetic relationships (Rye et al., 1998).

The estimated heritability and dominance genetic variance values of the body weight of 42-day-old females (BW42f), body weight at an age of 200 days females (BW200f), the body weight of 42-day-old males (BW42m), body weight at an age of 200 days males (BW200m), a total of 7,934 records for line 1 and 7,214 records for line 2 from 21 generations are shown in Table 6. The estimates are similar in both lines. The calculated values are high BW42m and BW200m, medium for BW42f and slight for BW200f. The magnitude of heritability was higher than for a larger parental dominance variance (Table 6). Surprisingly, high estimates of dominance values were reported for the body weight at an age of 42 days for both lines. This may be because of the fact that unknown environmental effects influenced on the early growth rate of the quails; a second explanation for the overestimation mentioned above may be the fact that the parental dominance variance includes maternal, common environmental and epistatic variances; and last but not least, a third reason might be the insufficient amount of data (Mielenz et al., 2006). Any estimation of the dominance variance requires much larger datasets than an estimation of the additive variance (Misztal et. al., 1997). Additionally, the high dominance variance estimates for BW may be due to the change of the allele frequencies caused by the selection of the egg weight over more than 20 generations (Mielenz et al., 2006). Using the dominance model to get a more precise estimation of heritability in a narrow sense should be applied.

Heritability and dominance genetic variance on harvest weight in two populations of Oncorhynchus kisutch, forming two classes such as odd and even-year spawners were also estimated. A high heritability for harvest weight was estimated in both populations but heritabilities decreased to even and odd populations moderately. Interestingly, the magnitude of the dominance variance was significantly decreased in both populations. In fact, the magnitude of these effects may be very different in different populations. However, ranking of the 30 best males and the 100 best females per generation changed when a high dominance variance was estimated, as was the case in one of the two populations (even) and dominance and common environmental variance may be important components of variance in harvest weight in O. kisutch, thus not including them may produce an overestimation of the predicted response; moreover, genetic evaluation was seen to be partially affected, since the ranking of selected animals changed with the inclusion of non-additive effects in the animal model (Gallardo et al., 2010).

Table 7. Additive and dominance components of reproductive traits in poultry

No.	References	Animal	Data size	Traits	Dominance effect	Heritability
1	Wei et al., 1993	Poultry	6001 (line1)	EN1	0.11±0.05	0.52±0.06
				EN2	0.15±0.06	0.35±0.05
				EN3	0.15±0.05	0.36±0.06
				EW1	0.01±0.05	0.55±0.06
				EW2	0.06±0.04	0.63±0.05
				ESG1	0.08±0.05	0.31±0.04
				ESG2	0.01±0.04	0.39±0.05
			12610 (line2)	EN1	0.10±0.05	0.48±0.04
				EN2	0.20±0.06	0.28±0.04
				EN3	0.18±0.06	0.35±0.04
				EW1	0.07±0.04	0.41±0.05
				EW2	0.02±0.05	0.52±0.04
				ESG1	0.11±0.05	0.34±0.04
				ESG2	0.05±0.05	0.4±0.039
			10038 (line3)	EN1	0.19±0.06	0.33±0.05
				EN2	0.11±0.46	0.15±0.03
				EN3	0.16±0.05	0.12±0.03
				EW1	0.13±0.05	0.38±0.05
				EW2	0.04±0.05	0.48±0.05
				ESG1	0.13±0.05	0.33±0.04
				ESG2	0.05±0.04	0.32±0.04
2	Misztal et al., 2000	Laying hen	26265	EN1	0.00-0.13	0.32
				EN2	0.10-0.14	0.19
				EN3	0.01-0.08	0.14-0.18
				EW	0.08	0.64-0.65
				SS	0.13-0.14	0.23-0.24
3	Mielenz et al., 2006	Quails	7934 (line 1)	EN200	0.07±0.08	0.32±0.05
				EW1	0.22±0.08	0.56±0.02
				EW2	0.17±0.07	0.44±0.03
			7214(line 2)	EN200	0.12±0.11	0.16±0.05
				EW1	0.06±0.06	0.54±0.05
				EW2	0.45±0.12	0.24±0.06

EN1, EN2, and EN3 = transformed egg numbers produced between 18 and 25, 26 and 65, and 18 and 65 week of age; EW1 and EW2 = egg weights measured at 30 to 35 and 40 to 45 week; ESGl and ESGB = egg specific gravities measured at 30 to 35 and 40 to 45 week; (2)EN1 = eggs laid between 19 and 25 weeks; EN2 = 26 and 38 weeks; EN3 = 26 and 54 weeks; EW = egg weigh; SS = shell strength; (3) EN200 = egg production at an age of 42 to 200 days; EW1 = average egg weight for the first 11 weeks of their laying season; EW2 = the average egg weight from weeks 12 to 23.

The estimates of dominance variance and heritability for egg production traits are presented in Table 7. These traits were examined egg number (EN) produced at 18 to 25 (ENl), 26 to 65 (EN2), and 18 to 65 week of age (EN3); egg weight (EW) measured at 30 to 35 (EW1) and 40 to 45 week (EW2); and egg specific gravity (ESG) measured at 30 to 35 (ESG1) and 40 to 45 week (ESG2); egg production at an age of 42 to 200 days (EN200); average egg weight for the first 11 weeks of their laying season (EW1); the average egg weight from weeks 12 to 23 (EW2). Within three White Leghorn lines, estimates for dominance variance and heritability were similar. The heritability estimates were moderately high and mostly higher than the proportion of dominance variance compared to the total phenotypic variance. However, the proportion of dominance variance was larger than the heritability for EN3 (line

3) and the dominance estimates were also obtained in low level for all traits. The approximate standard errors for genetic estimates were small laying hens because in poultry the proportion of full sibs is high enough to detect dominance relationships precisely. Significant dominance variation was found for all egg production traits, especially egg number (Wei et al., 1993).

Estimates of dominance variance and heritability for five egg traits on 26265 laying hens were show in Table 7. A model for estimation of dominance variance should also include the full-sib or a similar effect, provided the data set is large (Misztal and Besbes, 2000). The estimates of the dominance variances heritability were changed slightly for the models on the group includes the number of eggs laid between 19 and 25 weeks (EN1), 26 and 38 weeks (EN2), and 26 and 54 weeks (EN3), the egg characteristic traits were average egg weight (EW) and shell strength (SS), both measured between 38 and 54 weeks of age. Three reasons may explain such a confounding. The first one is the low variability of EN2. This trait corresponds to the egg production during the peak period, when the lay intensity, above 90%, is approaching the biological limit of one egg per day per hen; the second reason is related to the mating structure, which is mainly hierarchical, and the last one, but not the least, is an insufficient amount of data (Misztal and Besbes, 2000).

The study of Mielenz et al. (2006) estimates the dominance variance and heritability for egg production traits of two lines of quails from a long-term selection. For 1,717 records (line 1) and 1,671 records (line 2) at the age of 42 to 200 days (EN200), on the average egg weight for the first 11 weeks of their laying season (EW1), on the average egg weight from weeks 12 to 23 (EW2), and on their body weight at an age of 200 days (BW200f). For on the average egg weight for the first 11 weeks of their laying season, the heritability values were similar but the dominance variances were different. For the first line, the respective ratio of the dominance variance to the phenotypic variance for EN200, EW1, EW1 were larger than those of the values for the second line. The estimated h^2 values for lines 1 and 2 from dominance models were smaller than those from the additive model. The differences between the heritability estimates were higher than dominance variance. The results were in accordance with reports for the egg production trait for chickens (Wei et al., 1993; Mielenz et al., 2003). According to Wei et al. (1993), any resemblance between relatives is partly due to dominance effects. Since the highest standard error was calculated for this estimated value (Table 7), the small sample size might be one explanation for the partial overestimation of dominance ratios of the egg weight trait (Mielenz et al., 2006). Therefore, it is reasonable to expect the existence of dominance variance for the egg weight as well.

3.4 Conclusion from the literature

Based on the numerous studies it can be concluded that dominance effects are important and should be included in animal models in the course of breeding value estimation. Neglecting dominance effects results in confounding that is the dominance effects will appear in other random effects such as additive genetic effects or permanent environmental effects thus breeding value estimation becomes less precise. However it has to be kept in mind that precise estimation of dominance effect requires large datasets and large number of full sibs.

4. Aims of study

The objective of this PhD work was twofold. The first objective was to define the structures of the "best" models for the traits of interest (litter size traits such as number born alive, number born dead and total number born) of the Pannon Large, Pannon White and Pannon Ka rabbit. The second objective was to accomplish a detailed genetic evaluation of the importance of the dominance effects in those Pannon rabbit breeds including estimation of variance components, prediction of breeding values and analysis of breeding value stability based on additive and non-additive models. The research hypotheses were that the different models had different fit of the reproductive data and the models extended with dominance effects predict breeding values for the analysed traits more precisely.

5. Material and methods

5.1. Data information

Data of this study was collected in three Pannon rabbit breeds Pannon White, Pannon Ka and Pannon Large between 1992-2016, 1999-2016 and 2004-2015, respectively at the experimental rabbit farm of the Kaposvár University. Two different datasets were used for every breed. After testing the cytoplasmic effects it turned out that they had no effect for the litter traits. Thus in the latter models (not containing these effects) the data cumulated in the meantime was also used. This is the reason that two different numbers are given for each trait. General development and management of the Pannon rabbit breeds were described by Matics et al. (2014). Descriptive statistics of the kindling records are given in Table 8. The analyzed reproductive traits were number of kits born alive (NBA), number of kits born dead (NBD) and total number of born kits (TNB). The information about pedigree in Pannon rabbits was also shown in Table 9.

Table 8. Descriptive statistics on litter size traits analyses in Pannon rabbit breeds

Breed	Trait	N	Mean	SD	Minimum	Maximum
Pannon Large	NBA	5830	8,58	3,19	1	19
		5913	8,69	3,16	1	20
	NBD	6278	1,20	2,41	0	18
		5990	0,82	1,68	0	15
	TNB	6278	9.17	3,42	1	20
		5990	9.40	3.32	1	21
Pannon White	NBA	21060	8,54	3,04	1	19
		20227	8,54	3,04	1	19
	NBD	21060	0,43	1,10	0	15
		20227	0,43	1,10	0	15
	TNB	21060	8,97	3,07	1	19
		20227	8,97	3,08	1	19
Pannon Ka	NBA	15146	9,23	3,17	1	20
		13847	9,27	3,12	1	20
	NBD	15833	0,72	1,92	0	17
		13852	0,43	1,14	0	15
	TNB	15801	9,57	3,28	1	21
		13847	9,70	3,16	1	21

NBA - Number of kids born alive, NBD - Number of kids born dead, TNB - Total number of kids born

Table 9. The pedigree of Pannon rabbit breeds

Breed	Period	Animal	Sire	Dam
Pannon Large	2004-2015	3664	686	1469
Pannon White	1992-2016	8545	1414	4926
Pannon Ka	1999-2016	5543	1096	3691

5.2. Molecular analyses

5.2.1. Sampling for molecular analysis

To determine maternal (founder) lineages from the pedigree and obtained 255 samples for molecular analysis we used procedure mag_sampl module implemented in the MaGelLan 1.0 (Maternal Genealogy Lineage analyser) software (Ristov et al. 2016; https://github.com /sristov/magellan.). Analysis was performed on a previously corrected pedigree utilizing the mag_sampl module of the same software. Overall, there were six, two and four maternal (founder) lineages in Pannon Large, Pannon Ka and Pannon White breed, respectively. The blood of several rabbits per each maternal lineage was further taken for molecular analysis. In this way we were able to analyze maternal lineage segregation consistency through the pedigree.

5.2.2 Molecular analysis

Following, the DNA was extracted from 31 Pannon Ka, 25 Pannon Large and 22 Pannon White blood samples using commercially available NucleoSpin Blood Kit according to manufacturer's protocol (Macherey-Nagel GmbH & Co. KG, Germany). A 332-bp fragment of the mitochondrial D-loop region was amplified by PCR using primers upper (5′-CACCATCAGCACCCAAAG-3′) (Melo-Ferreira et al., 2007) and lower (5′-ATTTAAGAGGAACGTGTGGG-3′) (Pierpaoli et al., 1999). PCRs were performed in a 25 μL volume containing 0.2 μM of each primer and using Emerald AMP GT PCR Master Mix (Takara Bio Inc, Japan) according to manufacturer's protocol. The amplification reactions were performed on a iCycler (Biorad, Germany) comprised of an initial denaturation at 95 ºC for 5 min, 38 cycles of denaturation at 95 ºC for 45 s, annealing at 52 ºC for 45 s and extension at 72 ºC for 1 min and final extension at 72ºC for 1 min. PCR products were purified using Wizard SV Gel and PCR Clean-Up Kit (Promega, USA) and sequenced directly by using an ABI PRISM® 3100-Avant Genetic Analyzer and the BigDye- terminator method using both PCR primers. The sequences were visualized and aligned using MEGA 7 (Kumar et al., 2015). Haplotypes were calculated using DNA Sp 5.10 (Librado and Rozas, 2009) and Median-joining network (Bandelt et al., 1999) was constructed by PopART (Leigh and Bryant, 2015; http://popart.otago.ac.nz).

D-loop mtDNA sequences of Pannon rabbits were deposited in GenBank under the Accession numbers KY977609-KY977686.

5.2.3. Maternal pedigree verification (Maternal lineage segregation pedigree consistency)

Originally, only two haplotypes (D-loop mtDNA sequences), here named H1 and H2, were found in PL and PW while only H1 was found in PK population. We further imputed (assigned) obtained mtDNA sequences to the maternal lineages (*Mag_stat*) and consequently verified consistency of maternal lineage segregation through the pedigree (*Mag_verif*). Single conflict has been found in PL pedigree where H2, present in individual 13-20188 (YOB 2013), was not consistent with pedigree of three sequenced individuals. After identification, utilization of Mag_con_demo module as described in Čačić et al., (2014), and exclusion of non-consistent individual from the dataset only H1 was present in the PL breed. Thus, the difference between two haplotypes (H1 vs H2) for the litter size and growth traits was tested only in PW breed.

5.3 Models

5.3.1 Additive models with cytoplasmic and mtDNA haplotype effects and the fit of the models

To analyze the impact of cytoplasmic or mitochondrial (D-loop mtDNA) effects on the traits analysed we performed seven different models that are described in details in Table 10. The models (see Table 10) referred to the litter size traits and all had the same fixed effects known to have impact on their variability (Nagy et al., 2013a, Nagy et al., 2013b). Thus, as a fixed effect we modelled; parity (4 levels), year-month (101 levels-Pannon Large, 246 levels-Pannon White, 185 levels-Pannon Ka), inbreeding coefficient of dams (F_{Dam}) and litters (F_{Litter}). In all seven models permanent environment and additive genetic effects were treated as random effects while models were different due to the presence/absence of dam or sire or both - cytoplasmic or mitochondrial (D-loop mtDNA) effects, all treated as random effects. Here, in addition to the models with maternal lineage of dam effects, which is classical approach used in a large number of studies (Boettcher et al., 1996c, Boettcher et al., 1997; Snowder et al., 2004), we also modelled the maternal lineage of sire (bucks) effects. This decision was based on the established evidence that certain mitogenome mutations have strong impact on the male fertility (Ruiz-Pesinietal et al., 2000; John et al., 2005; Kumar and Sangeeta, 2009) and consequently can affect the litter size. We applied Model 5, 6 and 7 to tested variance contribution of the difference between Hap-1 and Hap-2. Applicable only in Pannon White breed.

The general structure of these models was:

$y = Xb + Za + Wp + e$

Where: y = vector of phenotypic observations, b=vector of fixed effects, a=vector of additive genetic effects, p= vector of individual permanent environmental effects, e= vector of residuals; X, Z, W incidence matrices linking phenotypic records to parameters.

Inbreeding coefficient of dams (F_{Dam}) and litters (F_{Litter}) were calculated with ENDOG 4.8 software (Gutiérrez and Goyache, 2005). The pedigree files did not contain all progeny of the does presented in the data set.

Table 10. Description of models used in estimating cytoplasmic and D-loop mtDNA effects

Models	1	2	3	4	5*	6*	7*
Fixed effects							
Parity (class variable)	x	x	x	x	x	x	x
Year_month (class variable)	x	x	x	x	x	x	x
F_{Dam} (covariable)	x	x	x	x	x	x	x
F_{Litter} (covariable)	x	x	x	x	x	x	x
Random effects							
Permanent	x	x	x	x	x	x	x
Additive	x	x	x	x	x	x	x
Maternal lineages of dames	-	x	-	x	-	-	-
Maternal lineages of sires	-	-	x	x	-	-	-
Haplotypes of mothers	-	-	-	-	x	-	x
Haplotypes of sires	-	-	-	-	-	x	x

*Reduced dataset as the number of known haplotypes following maternal segregation was smaller. F_{Dam} and F_{Litter} are inbreeding coefficients of dam and litter, respectively.

Thus, before calculation of litter inbreeding coefficients, dummy progeny was created according to the unique combinations of their parents (does and related mating bucks) and then litter inbreeding coefficients were calculated.

In order to compare the goodness of fit of the models the PREDICTION procedure of PEST (Groeneveld, 1990) was applied to calculate the mean squared error (MSE), bias and correlation between the observed and predicted values.

$$MSE = \frac{1}{n}\sum(\hat{y}_i - y_i)^2$$

Where: $\hat{y}_i$ and y_i are the predicted and observed phenotypic values. The prediction for a given kindling record of a given rabbit doe is accomplished summing all its BLUP.

Besides, the goodness-of-fit of these models also was assessed by using the log-likelihood value and Akaike's information criterion (AIC) (Posta J, 2008). AIC was calculated by:

*AIC= -2*log (maximum likelihood) + 2*(number of model parameters)*

The model with the lowest AIC was considered as best fitting model.

5.3.2 Additive models without cytoplasmic and mtDNA haplotype effects and the fit of the models

Applying single-trait animal models, genetic parameters, breeding values and genetic trends of NBA, NBD and TNB for Pannon breeds were estimated by the REML and BLUP methods using the PEST (Groeneveld, 1990) and VCE6 software (Groeneveld et al., 2008). Based on the available environmental factors, 12 different models were tested for all traits (Table 11) to estimate additive, permanent environmental, residual variances and breeding values.

Table 11. Fixed factors of applied models of Pannon rabbits

	Model											
Fixed effects	1	2	3	4	5	6	7	8	9	10	11	12
Parity	x	x	x	x	x	x	x	x	x	x	x	x
Age	-	x	-	-	x	-	-	x	-	-	x	-
Age_square	-	-	x	-	-	x	-	-	x	-	-	x
Year	x	x	x	x	x	x	-	-	-	-	-	-
Month	x	x	x	-	-	-	-	-	-	-	-	-
Season	-	-	-	x	x	x	-	-	-	-	-	-
Year_month	-	-	-	-	-	-	x	x	x	-	-	-
Year_season	-	-	-	-	-	-	-	-	-	x	x	x
Random effects												
Animal	x	x	x	x	x	x	x	x	x	x	x	x
Permanent environmental	x	x	x	x	x	x	x	x	x	x	x	x

Parity: parity number; Age: age of does at kindling; Age_square: the squared age of does at kindling; Year: year of kindling; Month: month of kindling; Season: season of kindling; Year_month: year and month of kindling; Year_season: year and season of kindling

The general structure of these models were:

$$y = Xb + Zpe + Wa + e$$

Where: y - vector of phenotypic observations; b - vector of fixed effects; pe - vector of permanent environmental effects; a - vector of additive genetic effects; e - vector of residuals: X, Z, W - incidence matrices linking phenotypic records to respective effects. In order to compare the goodness of fit of the models, the evaluation are the same used in the preceding (5.3.1) section.

5.3.3 Non-additive models

After determining the best fitted models for the analyzed breeds, dominance was included in these best models of the different litter size traits via the family class effect following the work of Hoeschele and Van Raden (1991):

$$y = Xb + Zpe + Wa + Uc + e$$

Where: c - vector of family class effects - dominant effect, U - incidence matrices linking phenotypic records to family effects. The other effects were the same as explained for the basic models (5.2.1 study). In addition to estimated variance components, dominance variance was calculated as $V_D = 4V_C$. Contributions of additive (h^2), dominance (d^2), and permanent environmental (p^2) variance to total phenotypic variance ($V_P = V_{Pe} + V_A + V_D + V_E$) were also calculated. V_E had to be corrected by 3/4 V_D because of the use of V_D instead of V_C.

5.4. Genetic trends

The squared differences between the observed and predicted values based on the 12 models were compared by means of one-way ANOVA (R Core Team, 2012). Genetic trends of additive and non-additive effects were determined by fitting the average predicted breeding values of the animals born in the same year on the years of birth using linear regression. The obtained slopes for two datasets were compared as described by Mead et al. (1993) as follows:

$$F = \frac{[RSS(a,b) - RSS(a_1,b_1,a_2,b_2)]/2}{RSS(a_1,b_1,a_2,b_2)/(n_1+n_2-4)}$$

Where: F-distribution to test the hypothesis that there is no difference between the two linear regressions; RSS (a, b) is residual sum of squares of combined datasets 1 and 2 with degree of freedom (d.f) = 2; RSS (a_1, b_1, a_2, b_2) is sum of residual variations of data 1 with d.f = n_1-2 and data 2 with d.f = n_2-2.

5.5. Stability of breeding values

Following the method used by Nagy et al. (2013b) the stability of evaluated breeding values using the different models was evaluated with Spearman rank correlations and also by comparing the concordance between the top-ranked 100 rabbits across the models. Ranking the animals was performed and according to each models 100 rabbits with the highest breeding values were selected. Then it was analysed that among the best rabbits how many common animals can be found.

6. Results and discussion

6.1 Descriptive statistics

Means and standard deviations of NBA and TNB of the analyzed breeds (Table 8) showed the highest value for Pannon Ka breed (maternal line) what was expected as this population is more intensively selected for the litter size traits then it is Pannon White or Pannon Large population. However, the observed litter size values were close to those reported previously (Al-Saef et al., 2008; Nagy et al., 2011a; Nagy et al., 2011b; Nagy et al., 2013a; Nagy et al., 2014). The different line graphs of the phenotypic mean of NBA, NBD and TNB in the subsequent months, years and parities in Pannon rabbits from 1992 to 2016 were shown in Figure 1-9.

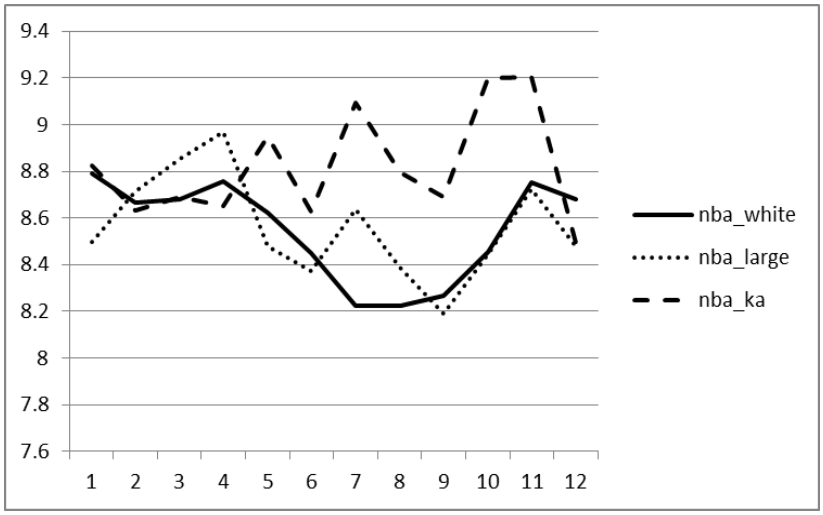

Figure 1. The phenotypic mean of NBA in the subsequent months in Pannon rabbits

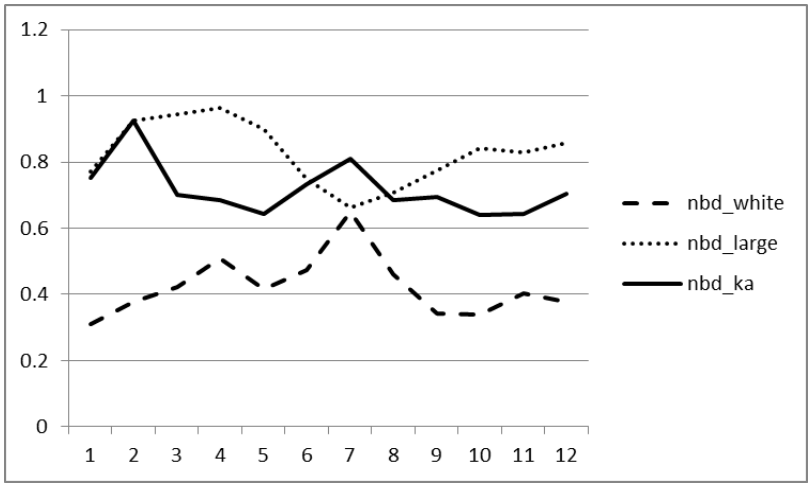

Figure 2. The phenotypic mean of NBD in the subsequent months in Pannon rabbits

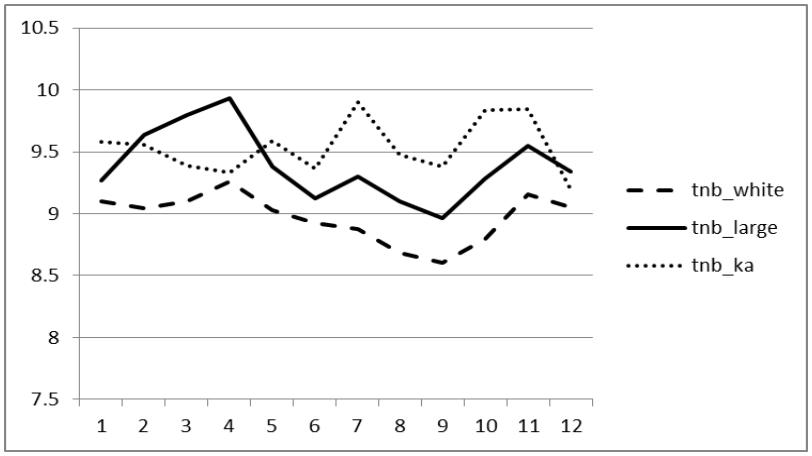

Figure 3. The phenotypic mean of TNB in the subsequent months in Pannon rabbits

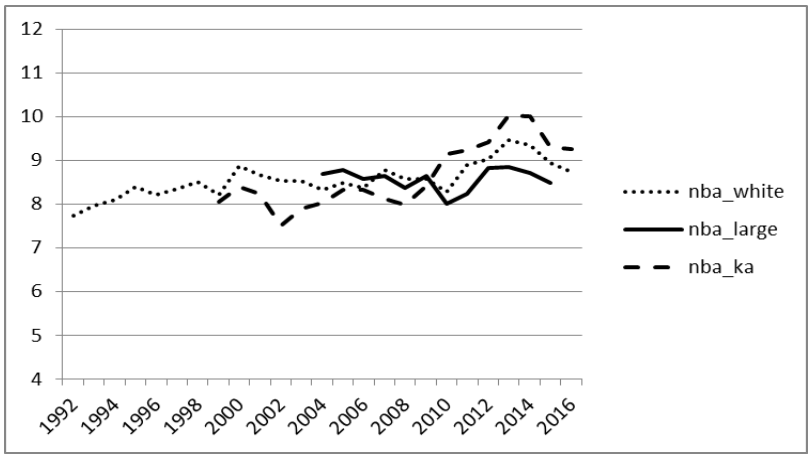

Figure 4. The phenotypic mean of NBA in the subsequent years in Pannon rabbits

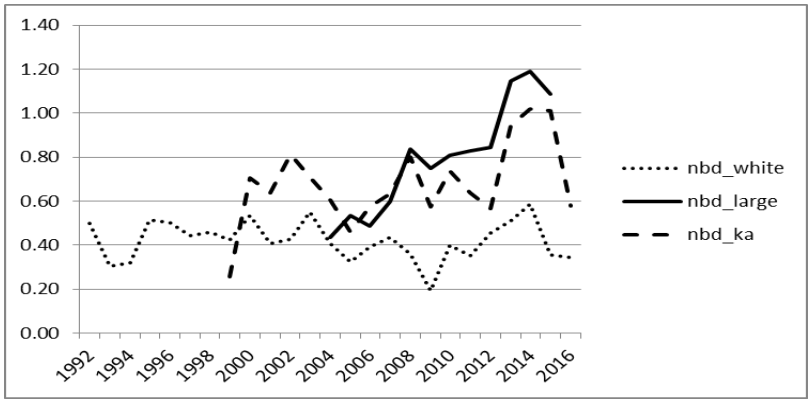

Figure 5. The phenotypic mean of NBD in the subsequent years in Pannon rabbits

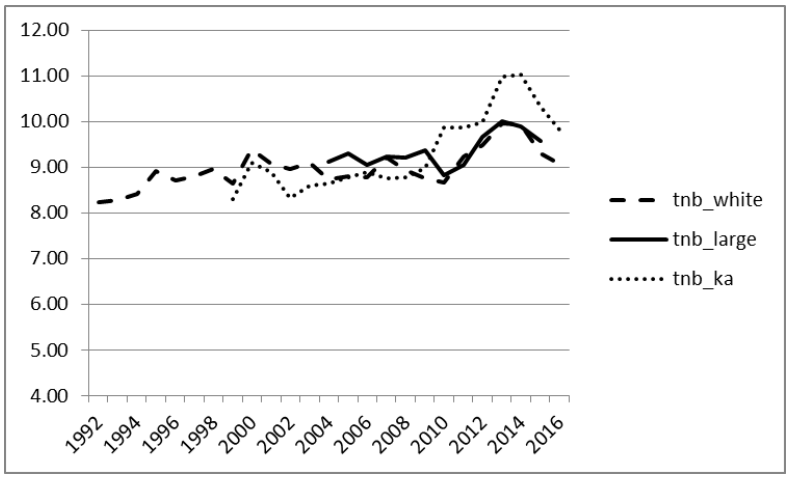

Figure 6. The phenotypic mean of TNB in the subsequent years in Pannon rabbits

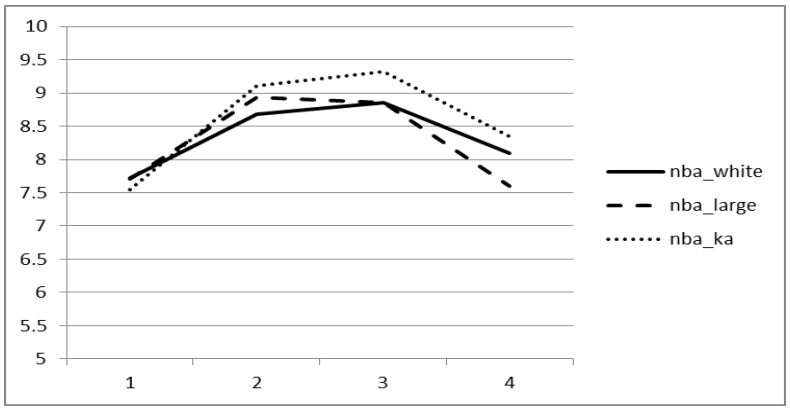

Figure 7. The phenotypic mean of NBA in the subsequent parities in Pannon rabbits

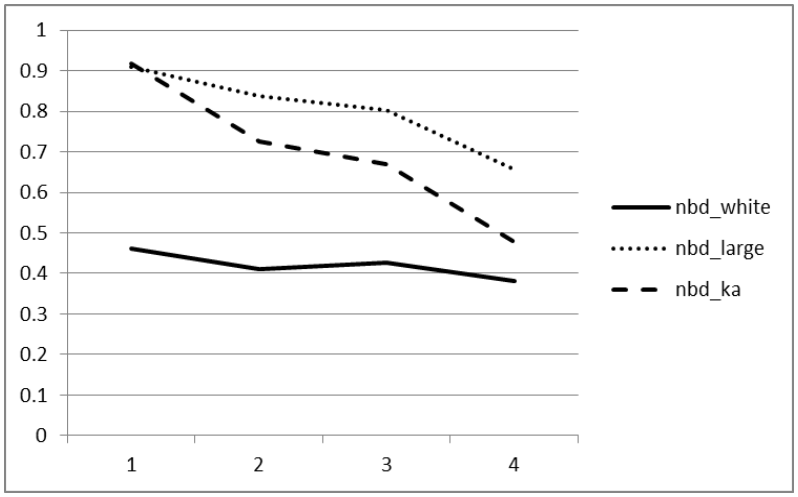

Figure 8. The phenotypic mean of NBD in the subsequent parities in Pannon rabbits

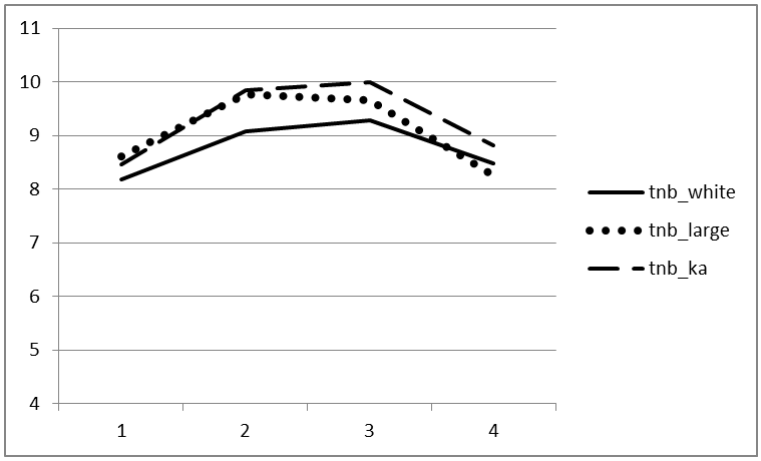

Figure 9. The phenotypic mean of TNB in the subsequent parities in Pannon rabbits

6.2 D-loop mtDNA diversity

The variability of D-loop mtDNA polymorphism in three Pannon Rabbit breeds was extremely low as in PK and PL as only one haplotype (H1) was found while in PW only two haplotypes, H1 (76%) and H2 (24%), were identified. The phylogenetic position of two haplotypes (H1 and H2) found in Pannon rabits is presented in Figure 10.

While separated by 13 mutations, haplotypes H1 and H2 were grouped within two most common haplotypes (see Figure 10). This heterogeneity of maternal origin is in accordance with the formation history of the breed as PW is a synthetic breed derived from two breeds, the Californian and New Zealand rabbits. H1 is by far the most represented haplotype in rabbits and a number of very diverse rabbit populations share this haplotype (Asian domestic, Australian wild, European domestic and European wild). H2 is the second most frequent

haplotype with sequences found in Australian wild, European domestic and European wild populations. Description of rabbit (Oryctolagus cuniculus) haplotype sequences presented in Figure 10. Further details are given in Annex.

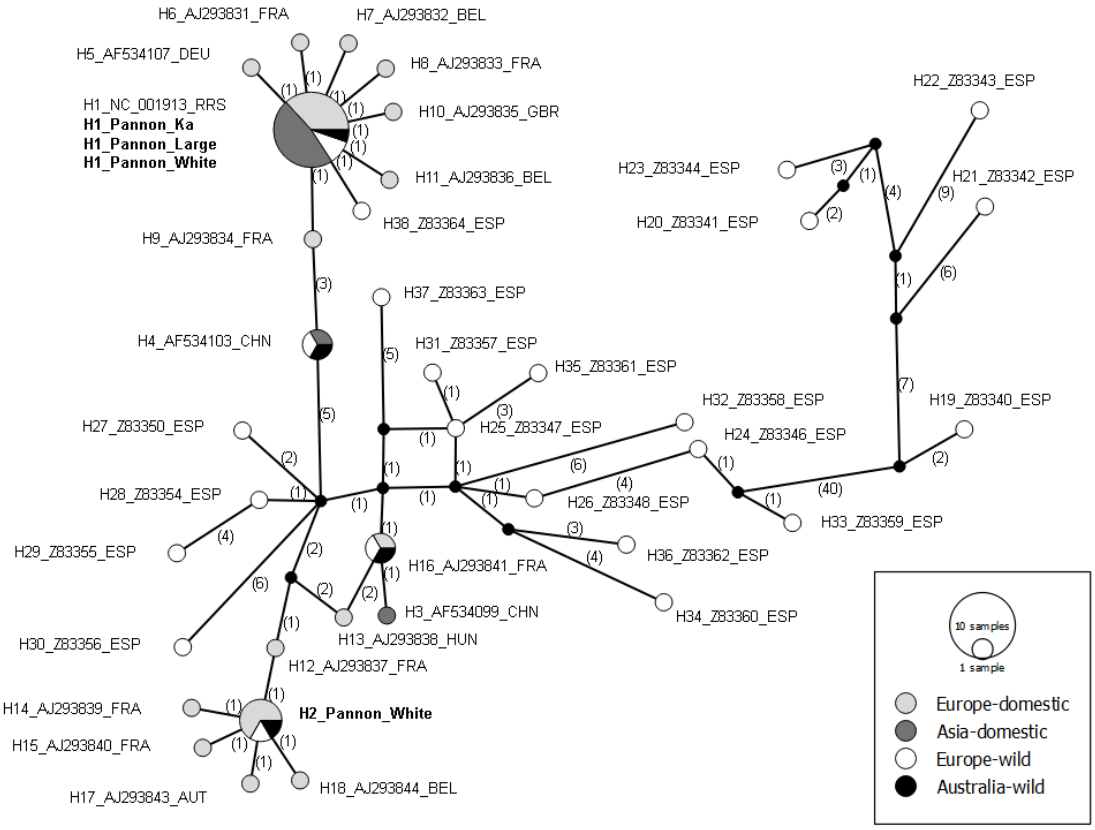

Figure 10. Median-joining network diagram showing phylogenetic positions of haplotypes found in Pannon Ka, Pannon Large and Pannon White rabbits with respect to haplotypes found in other wild and domestic rabbit populations (see the legend for a detailed description)**.** Diagram was constructed based on mtDNA haplotypes identified by polymorphism analysis of a 332-bp fragment of mtDNA (RRS: NC001913 positions 15492–15824). Circles are proportional to haplotype frequency, the black points represent hypothetical sequences that were not observed, while the number of mutations separating nodes are given near branches in parentheses. Names of the presented haplotypes contain identification, accession number and origin (abbreviation) with the exception of Pannon breeds that are given by full name.

6.3 Models

6.3.1 Additive models with cytoplasmic and mtDNA haplotype effects and the fit of the models

Estimates additive genetic variances, cytoplasmic (maternal-paternal) or D-loop mtDNA (maternal-paternal), permanent environmental and residual variances by the magnitude and ratios (compared to the phenotypic variance) are summarized in Tables 12-15 for litter traits. The best model fits (smallest MSE values) were obtained in models with cytoplasmic effects. Note that in Model 5, 6 and 7 in Pannon White rabbits sample sizes were reduced. However, both, estimated cytoplasmic effects (maternal - $mcyt^2$ and paternal - $pcyt^2$) were from zero (0.0%), to negligible (0.3% ± 0.003) obtained for $pcyt^2$ for NBA in Pannon Ka). The similar results for D-loop mtDNA effects were negligible 0.1% ± 0.001 (maternal - Hma^2) and 0.02-0.1% ± 0.003-0.001 (paternal - Hpa^2). Not different results, tiny variance and non-significance, were obtained when we analysed the difference between two mtDNA haplotypes (Table 15). The estimated heritabilities of Pannon rabbits were small and ranged 0.071 - 0.088 ± 0.01 (NBA), 0.02 - 0.047 ± 0.01 (NBD) and 0.068 - 0.101 ± 0.01 (TNB). The similar trend for ratios of the permanent environmental variance to the phenotypic variance ranged for NBA (0.075–0.126 ± 0.01), for NBD (0.000-0.020 ± 0.01) and for TNB (0.072–0.118±0.01) in those breeds.

Table 12. Estimated variance components and genetic parameters for additive genetic, cytoplasmic (maternal and paternal) and environmental effects for litter size traits in Pannon Large breeds

Traits	Model	V_A	h^2	V_{mcyt}	$mcyt^2$	V_{pcyt}	$pcyt^2$	V_{pe}	p^2	V_E	e^2	MSE	AIC
	1	0.852	0.088	-	-	-	-	1.220	0.126	7.630	0.786	6.694	-5622
	2	0.853	0.088	0.000	0.000	-	-	1.219	0.126	7.630	0.786	6.694	-5598
NBA	3	0.853	0.088	-	-	0.000	0.000	1.219	0.126	7.630	0.786	6.694	-5598
	4	0.853	0.088	0.000	0.000	0.000	0.000	1.219	0.126	7.630	0.786	6.694	-5574
	1	0.088	0.032	-	-	-	-	0.036	0.013	2.624	0.955	2.492	-6692
	2	0.088	0.032	0.000	0.000	-	-	0.036	0.013	2.624	0.955	2.492	-6668
NBD	3	0.087	0.032	-	-	0.004	0.001	0.034	0.012	2.624	0.954	2.491	-6663
	4	0.087	0.032	0.000	0.000	0.004	0.001	0.037	0.012	2.624	0.954	2.491	-6639
	1	0.877	0.083	-	-	-	-	1.250	0.118	8.466	0.799	7.466	-5667
	2	0.880	0.083	0.000	0.000	-	-	1.250	0.118	8.464	0.799	7.466	-5643
TNB	3	0.878	0.083	-	-	0.000	0.000	1.250	0.118	8.465	0.799	7.465	-5643
	4	0.878	0.083	0.000	0.000	0.000	0.000	1.250	0.118	8.465	0.799	7.465	-5619

NBA - Number of kids born alive; NBD - Number of kids born dead; TNB - Total number of kids born; h^2 is narrow sense heritability (V_A/V_P); $mcyt^2$ is the contribution of cytoplasmic maternal variance to the phenotypic variance ($Vmcyt/V_P$); $pcyt^2$ is the contribution of cytoplasmic paternal variance to the phenotypic variance ($Vpcyt/V_P$); p^2 is the contribution of permanent environmental variance to the phenotypic variance (V_{Pe}/V_P); e^2 is the contribution of residual variance to phenotypic variance (V_E/V_P); MSE is mean squared error; AIC: Akaike's information criterion

Table 13. Estimated variance components and genetic parameters for additive genetic, cytoplasmic (maternal and paternal) and environmental effects for litter size traits in Pannon White breeds

Traits	Model	V_A	h^2	V_{mcyt}	$mcyt^2$	V_{pcyt}	$pcyt^2$	V_{pe}	p^2	V_E	e^2	MSE	AIC
	1	0.674	0.076	-	-	-	-	0.713	0.080	7.529	0.844	6.812	-23772
	2	0.674	0.076	0.000	0.000	-		0.712	0.080	7.529	0.844	6.812	-23518
NBA	3	0.672	0.075	-	-	0.012	0.001	0.710	0.080	7.523	0.844	6.802	-23596
	4	0.672	0.075	0.000	0.000	0.012	0.001	0.711	0.080	7.523	0.844	6.802	-23342
	1	0.024	0.020	-	-	-	-	0.024	0.020	1.135	0.960	1.086	-25993
	2	0.024	0.020	0.000	0.000	-	-	0.024	0.020	1.135	0.960	1.086	-25739
NBD	3	0.024	0.020	-	-	0.000	0.000	0.024	0.020	1.135	0.960	1.086	26390
	4	0.024	0.020	0.000	0.000	0.000	0.000	0.024	0.020	1.135	0.960	1.086	-25569
	1	0.695	0.076	-	-	-	-	0.760	0.083	7.652	0.840	6.910	-23547
	2	0.695	0.076	0.000	0.000	-	-	0.760	0.084	7.652	0.840	6.910	-23293
TNB	3	0.694	0.076	-	-	0.005	0.001	0.759	0.083	7.649	0.840	6.906	-23376
	4	0.694	0.076	0.000	0.000	0.005	0.001	0.759	0.083	7.649	0.840	6.906	-23122

NBA - Number of kids born alive; NBD - Number of kids born dead; TNB - Total number of kids born; h^2 is narrow sense heritability (V_A/V_P); $mcyt^2$ is the contribution of cytoplasmic maternal variance to the phenotypic variance ($Vmcyt/V_P$); $pcyt^2$ is the contribution of cytoplasmic paternal variance to the phenotypic variance ($Vpcyt/V$); p^2 is the contribution of permanent environmental variance to the phenotypic variance (V_{Pe}/V_P); e^2 is the contribution of residual variance to phenotypic variance (V_E/V_P); MSE is mean squared error; AIC: Akaike's information criterion.

Table 14. Estimated variance components and genetic parameters for additive genetic, cytoplasmic (maternal and paternal) and environmental effects for litter size traits in Pannon Ka breeds

Traits	Model	V_A	h^2	V_{mcyt}	$mcyt^2$	V_{pcyt}	$pcyt^2$	V_{pe}	p^2	V_E	e^2	MSE	AIC
	1	0.754	0.087	-	-	-	-	0.647	0.075	7.270	0.838	6.545	-13623
	2	0.755	0.087	0.000	0.000	-	-	0.647	0.075	7.270	0.838	6.544	-13586
NBA	3	0.760	0.087	-	-	0.000	0.000	0.647	0.075	7.270	0.838	6.544	-13583
	4	0.760	0.087	0.000	0.000	0.027	0.003	0.644	0.074	7.266	0.835	6.539	-13545
	1	0.060	0.047	-	-	-	-	0.000	0.000	1.217	0.953	1.163	-17489
	2	0.060	0.047	0.000	0.000	-	-	0.000	0.000	1.217	0.953	1.163	-17451
NBD	3	0.060	0.047	-	-	0.000	0.000	0.000	0.000	1.217	0.953	1.163	-17449
	4	0.060	0.047	0.000	0.000	0.000	0.000	0.000	0.000	1.217	0.953	1.163	-17411
	1	0.885	0.100	-	-	-	-	0.638	0.072	7.288	0.827	6.542	-13176
	2	0.887	0.101	0.000	0.000	-	-	0.637	0.072	7.289	0.827	6.542	-13138
TNB	3	0.887	0.101	-	-	0.000	0.000	0.638	0.072	7.289	0.827	6.542	-13136
	4	0.887	0.101	0.000	0.000	0.000	0.000	0.638	0.072	7.288	0.827	6.542	-13098

NBA - Number of kids born alive; NBD - Number of kids born dead; TNB - Total number of kids born; h^2 is narrow sense heritability (V_A/V_P); $mcyt^2$ is the contribution of cytoplasmic maternal variance to the phenotypic variance ($Vmcyt/V_P$); $pcyt^2$ is the contribution of cytoplasmic paternal variance to the phenotypic variance ($Vpcyt/V_P$); p^2 is the contribution of permanent environmental variance to the phenotypic variance (V_{Pe}/V_P); e^2 is the contribution of residual variance to phenotypic variance (V_E/V_P); MSE is mean squared error; AIC: Akaike's information criterion.

Although encoding for a small number of genes, effects of mitogenome variation on production traits are reported in a number of animal domestic species. On the other side, the impact of mitogenome on production traits was never analysed in rabbits. In this study we analysed the effects of mitogenome variation on litter size traits (NBA, NBD and TNB). We started our analysis by testing cytoplasmic effects on production traits, where the impact of maternal lineages was analysed for both does and mating bucks. For all traits and breeds the impact of cytoplasmic inheritance was absent or negligible. In all three Pannon breeds we further determined D-loop mtDNA haplotypes for each maternal lineage. Overall, there was only two different haplotypes present in PW (H1 and Hap-2) while in other two breeds (PK and PL) only H1 was present if we exclude a small number of rabbits in PK breed with non-consistent mtDNA segregation in a pedigree. We also did not found significant contribution of D-loop mtDNA sequence polymorphism on any of production traits analysed in PW. The lack of complete mitogenome polymorphism, as suggested from the analysis performed on the D-loop mtDNA sequence, is the most likely explanation for the observed results. Our molecular analysis was restricted only to 332 bps and it is possible, that complete mitogenome sequence variation is higher than observed for D-loop mtDNA sequence (332 bps). However, although this needs to be confirmed, we think that additional complete mitogenome sequencing would not affect results obtained in this study. On a 332 bp long sequence haplotypes (H1 and H2) do belong to the most common haplotypes in rabbits.

However, we are not able to say if segregating mitogenome variation is optimal with respect to production traits as well as that they are free of detrimental mutations. Thus, the magnitude of potential benefits of the introduction or alteration of mitogenome variation in the rabbit breeding remains an open question for future research.

Table 15. Estimated variance components for additive genetic, D-loop mtDNA (maternal and paternal) and environmental effects for litter size traits in Pannon White rabbit

Traits	Model	V_A	h^2	V_{Hma}	Hma^2	V_{Hpa}	Hpa^2	V_{pe}	p^2	V_E	e^2	MSE	AIC
NBA	5	0.606	0.071	0.000	0.000	-	-	0.736	0.086	7.252	0.844	6.463	-5872
	6	0.617	0.071	-	-	0.006	0.001	0.716	0.083	7.310	0.845	6.402	-5872
	7	0.652	0.074	0.009	0.001	0.000	0.000	0.739	0.084	7.415	0.841	6.459	-5922
NBD	5	0.038	0.031	0.000	0.000	-	-	0.008	0.006	1.193	0.963	1.131	-6696
	6	0.029	0.023	-	-	0.0001	0.0001	0.020	0.016	1.211	0.962	1.140	-6696
	7	0.035	0.027	0.000	0.000	0.000	0.000	0.015	0.012	1.251	0.961	1.168	22748
TNB	5	0.602	0.068	0.00000	0.00000	-	-	0.817	0.093	7.377	0.839	6.559	-5720
	6	0.628	0.070	-	-	0.002	0.0002	0.818	0.092	7.474	0.838	6.518	-5719
	7	0.637	0.070	0.005	0.001	0.000	0.000	0.833	0.092	7.601	0.838	6.611	-5754

NBA - Number of kids born alive; NBD - Number of kids born dead; TNB - Total number of kids born; h^2 is narrow sense heritability (V_A/V_P); Hma^2 is the contribution of D-loop mtDNA mother haplotype variance to the phenotypic variance (V_{Hma}/V_P); Hpa^2 is the contribution of D-loop mtDNA father haplotype variance to the phenotypic variance (V_{Hpa}/V_P); p^2 is the contribution of permanent environmental variance to the phenotypic variance (V_{Pe}/V_P); e^2 is the contribution of residual variance to phenotypic variance (V_E/V_P); MSE is mean squared error; AIC: Akaike's information criterion.

6.3.2 Additive models without cytoplasmic and mtDNA haplotype effects and the fit of the models

6.3.2.1 Pannon Large breed

The magnitude and ratios (compared to the phenotypic variance) of additive genetic, permanent environmental and residual variance components are presented in Tables 16-18. The various heritability estimates were low for NBA and TNB ranging from 0.03 to 0.07 and close to zero for NBD ranging from 0.01 to 0.02. The different models did not result in substantially different heritability estimates, although it could be noted that adding age or age-square (models 2, 3, 5, 6, 8, 9, 11, 12) consistently reduced residual variance components of NBA and TNB. The obtained NBA, NBD and TNB heritability estimates in this study were within the ranges (0.03-0.13 for NBA, 0.02-0.04 for NBD and 0.08-0.15 for TNB) reported in relevant literature (Moura et al., 2001; García and Baselga, 2002b; Mantovani et al., 2008; Nagy et al., 2013a; Nagy et al., 2014). The variability in the heritability estimates of these studies may be caused by genetic differences between the analysed rabbit breeds. As it was observed by Rastogi et al. (2000), rabbit populations with heterogeneous history involving multiple breed introductions (e.g. in tropical environments) may show higher heritability values. Another source for different heritabilities might be connected with the different structures of the applied animal models. With some simplification model structures in different studies may be sorted into two main groups. One group may comprise the models containing very similar random (animal and permanent environmental effects) and fixed effects (year-month or year-season and parity) as in the present study (Rastogi et al., 2000; Moura et al., 2001; Al-Saef et al., 2008). In the other group the so-called physiological status of the doe (when pregnant, the doe may be nulliparous, lactating or not lactating) is used instead of or together with the parity effect (García and Baselga, 2002a; García and Baselga, 2002b; Garreau et al., 2005; Piles et al., 2006; Lenoir and Garreau, 2009; Lenoir et al., 2011). Apart from these random and fixed effects some authors also included maternal genetic effects (Moura et al., 2001), the mating buck as a random effect (Rastogi et al., 2000; Piles et al., 2006; Nagy et al., 2011b), the inbreeding coefficient of the doe (Moura et al., 2001, Nagy et al., 2013a) and the inbreeding coefficient of the litter (Nagy et al., 2013a) as covariates. Nevertheless, most studies used only one model for genetic parameter estimation, therefore no tendency could be detected between the used model structure and the received heritability estimates. The estimates for the ratios of the permanent environmental variance to the phenotypic variance were low for NBD and moderate for NBA and TNB and they exceeded

those of the additive genetic effects. These estimates were within the range of values (0.03-0.18 for NBA; 0.01-0.07 for NBD and 0.08-0.13 for TNB) given by other previously mentioned authors (García and Baselga, 2002a; Garcia and Baselga, 2002b; Ragab et al., 2011; Nagy et al. 2011a; Nagy et al., 2013a; Nagy et al., 2014). However, based on the estimated variance components for NBA, NBD and TNB there was no clear tendency in the literature to show if the additive genetic or the permanent environmental effects represents a greater proportion of the phenotypic variance.

The goodness of fit values for the used models developed for the studied traits are presented in Tables 16-18. Based on the MSE values of the observed and predicted NBA, NBD and TNB, the models containing age or age square showed a better goodness of fit when compared to the other models. Bias values were practically zero for all traits and models. When comparing squared differences between the observed and predicted values based on the 12 models, we see that they were highly significant for NBA and TNB ($p<0.0001$), respectively, but they were non-significant for NBD ($p=0.7$). Based on the parameters evaluating the goodness of fit for different models, model 8 was selected for NBA and TNB as the "best" model. For the sake of simplicity, model 8 was also chosen for NBD (where the fit of the models was not different). Unfortunately, no similar analysis was available in the literature. Using the performance records of the Pannon White and Pannon Ka rabbits, Nagy et al. (2011b) applied MSE of the observed and predicted NBA and TNB when comparing repeatability and multivariate models. The repeatability model of Nagy et al. (2011b) had the same structure as model 8 of the present study. When comparing model 8 of the present study and the repeatability models of Nagy et al. (2011b) it may be concluded that both studies showed MSE for NBA and TNB.

Table 16. Estimated variance components for the number of kits born alive (NBA) of PL

Model	V_A	h^2	V_{Pe}	p^2	V_E	e^2	MSE	AIC
1	0.77 ± 0.06	0.08 ± 0.018	1.10 ±0.05	0.11 ± 0.016	8.09 ± 0.04	0.81 ±0.012	7.28	-5425
2	0.78 ± 0.06	0.08 ± 0.019	1.41 ±0.05	0.15 ± 0.018	7.29 ±0.04	0.77 ±0.012	5.87	-4213
3	0.78 ± 0.06	0.08 ± 0.019	1.41 ±0.05	0.15 ± 0.018	7.29 ± 0.04	0.77 ±0.012	5.87	-4213
4	0.75 ± 0.06	0.07 ± 0.018	1.11 ±0.05	0.11 ± 0.016	8.12 ± 0.04	0.81 ±0.011	7.32	-5388
5	0.80 ± 0.06	0.08 ± 0.020	1.40 ±0.05	0.15 ± 0.018	7.30 ± 0.04	0.77 ±0.012	5.89	-4160
6	0.80 ± 0.06	0.08 ± 0.020	1.40 ±0.05	0.15 ± 0.018	7.30 ± 0.04	0.77 ±0.012	5.89	-4160
7	0.73 ± 0.06	0.07 ± 0.019	1.15 ±0.05	0.12 ± 0.016	7.98 ± 0.04	0.81 ±0.012	7.07	-5527
8	0.70 ± 0.07	0.07 ± 0.021	1.51 ±0.06	0.16 ± 0.019	7.22 ± 0.04	0.77 ±0.012	5.72	-4352
9	0.70 ± 0.07	0.07 ± 0.021	1.51 ±0.06	0.16 ± 0.019	7.22 ± 0.04	0.77 ±0.012	5.72	-4352
10	0.80 ± 0.06	0.08 ± 0.019	1.09 ±0.05	0.11 ± 0.016	8.05 ± 0.04	0.81 ±0.012	7.21	-5451
11	0.77 ± 0.06	0.08 ± 0.020	1.42 ±0.05	0.15 ± 0.018	7.25 ± 0.04	0.77 ±0.012	5.82	-4239
12	0.77 ± 0.06	0.08 ± 0.020	1.42 ±0.05	0.15 ± 0.018	7.25 ± 0.04	0.77 ±0.012	5.82	-4239

Model 1: with additive, parity, permanent environmental, year and month effects; Model 2: as in model 1, plus age effects; Model 3: as in model 1, plus age square effects; Model 4: with additive, parity, permanent environmental, year and season effects; Model 5: as in model 4, plus age effects; Model 6: as in Model 4, plus age square effects; Model 7: with additive, parity, permanent environmental and year-month effects; Model 8: as in model 7, plus age effects; Model 9: as in model 7, plus age square; Model 10: with additive, parity, permanent environmental and year-season effects; Model 11: as in model 10, plus age effects; Model 12, as in model 10, plus age square effects; V_A, V_{Pe} and V_E are additive, permanent environmental, and residual variances, respectively; h^2 is narrow sense heritability (V_A/V_P); p^2 is the contribution of permanent environmental variance to phenotypic variance (V_{Pe}/V_P); e^2 is the contribution of residual variance to phenotypic variance (V_E/V_P); MSE: mean squared error; AIC: Akaike's information criterion.

Table 17. Estimated variance components for the number of kits born dead (NBD) of PL

Model	V_A	h^2	V_{Pe}	p^2	V_E	e^2	MSE	AIC
1	0.11 ± 0.02	0.02 ± 0.009	0.38 ± 0.03	0.07 ± 0.014	5.13 ± 0.03	0.91 ± 0.013	4.81	-6348
2	0.09 ± 0.02	0.01 ± 0.009	0.34 ± 0.04	0.06 ± 0.015	5.23 ± 0.04	0.92 ± 0.013	4.51	-6000
3	0.09 ± 0.02	0.01 ± 0.009	0.34 ± 0.04	0.06 ± 0.015	5.23 ± 0.04	0.92 ± 0.013	4.51	-6000
4	0.11 ± 0.02	0.02 ± 0.009	0.38 ± 0.03	0.07 ± 0.014	5.14 ± 0.03	0.91 ± 0.013	4.82	-6282
5	0.09 ± 0.02	0.02 ± 0.009	0.34 ± 0.04	0.06 ± 0.015	5.24 ± 0.04	0.92 ± 0.013	4.53	-5942
6	0.09 ± 0.02	0.02 ± 0.009	0.34 ± 0.04	0.06 ± 0.015	5.24 ± 0.04	0.92 ± 0.013	4.53	-5942
7	0.10 ± 0.02	0.02 ± 0.009	0.41 ± 0.03	0.07 ± 0.014	5.06 ± 0.03	0.91 ± 0.013	4.67	-6484
8	0.07 ± 0.02	0.01 ± 0.009	0.38 ± 0.03	0.07 ± 0.014	5.18 ± 0.04	0.92 ± 0.012	4.40	-6108
9	0.07 ± 0.02	0.01 ± 0.009	0.38 ± 0.03	0.07 ± 0.014	5.18 ± 0.04	0.92 ± 0.012	4.40	-6108
10	0.12 ± 0.02	0.02 ± 0.009	0.39 ± 0.03	0.07 ± 0.014	5.12 ± 0.03	0.91 ± 0.013	4.78	-6331
11	0.09 ± 0.02	0.02 ± 0.009	0.35 ± 0.04	0.06 ± 0.015	5.21 ± 0.04	0.92 ± 0.013	4.48	-5978
12	0.09 ± 0.02	0.02 ± 0.009	0.35 ± 0.04	0.06 ± 0.015	5.21 ± 0.04	0.92 ± 0.013	4.48	-5978

Model 1: with additive, parity, permanent environmental, year and month effects; Model 2: as in model 1, plus age effects; Model 3: as in model 1, plus age square effects; Model 4: with additive, parity, permanent environmental, year and season effects; Model 5: as in model 4, plus age effects; Model 6: as in Model 4, plus age square effects; Model 7: with additive, parity, permanent environmental and year-month effects; Model 8: as in model 7, plus age effects; Model 9: as in model 7, plus age square; Model 10: with additive, parity, permanent environmental and year-season effects; Model 11: as in model 10, plus age effects; Model 12, as in model 10, plus age square effects; V_A, V_{Pe} and V_E are additive, permanent environmental, and residual variances, respectively; h^2 is narrow sense heritability (V_A/V_P); p^2 is the contribution of permanent environmental variance to phenotypic variance (V_{Pe}/V_P); e^2 is the contribution of residual variance to phenotypic variance (V_E/V_P); MSE: mean squared error; AIC: Akaike's information criterion.

Table 18. Estimated variance components, total number of born kits (TNB) of PL

Model	V_A	h^2	V_{Pe}	p^2	V_E	e^2	MSE	AIC
1	0.61 ± 0.05	0.05 ± 0.016	1.31 ± 0.05	0.11 ± 0.014	9.48 ± 0.04	0.83 ± 0.011	8.59	-5537
2	0.56 ± 0.06	0.05 ± 0.018	1.64 ± 0.05	0.15 ± 0.017	8.50 ± 0.04	0.79 ± 0.011	6.93	-4334
3	0.56 ± 0.06	0.05 ± 0.018	1.64 ± 0.05	0.15 ± 0.017	8.50 ± 0.04	0.79 ± 0.011	6.93	-4334
4	0.61 ± 0.05	0.05 ± 0.015	1.30 ± 0.05	0.11 ± 0.014	9.52 ± 0.04	0.83 ± 0.011	8.65	-5504
5	0.60 ± 0.06	0.06 ± 0.017	1.60 ± 0.05	0.15 ± 0.017	8.53 ± 0.04	0.79 ± 0.012	6.96	-4278
6	0.60 ± 0.06	0.06 ± 0.017	1.60 ± 0.05	0.15 ± 0.017	8.53 ± 0.04	0.79 ± 0.012	6.96	-4278
7	0.51 ± 0.05	0.05 ± 0.015	1.40 ± 0.05	0.12 ± 0.015	9.29 ± 0.04	0.83 ± 0.010	8.30	-5591
8	0.41 ± 0.05	0.04 ± 0.017	1.78 ± 0.05	0.17 ± 0.017	8.37 ± 0.04	0.79 ± 0.011	6.71	-4404
9	0.41 ± 0.05	0.04 ± 0.017	1.78 ± 0.05	0.17 ± 0.017	8.37 ± 0.04	0.79 ± 0.011	6.71	-4404
10	0.62 ± 0.05	0.05 ± 0.016	1.29 ± 0.05	0.11 ± 0.014	9.41 ± 0.04	0.83 ± 0.011	8.50	-5539
11	0.54 ± 0.05	0.05 ± 0.017	1.63 ± 0.05	0.16 ± 0.017	8.45 ± 0.04	0.80 ± 0.012	6.87	-4328
12	0.54 ± 0.05	0.05 ±0.017	1.63 ± 0.05	0.16 ± 0.017	8.45 ± 0.04	0.80 ± 0.012	6.87	-4328

Model 1: with additive, parity, permanent environmental, year and month effects; Model 2: as in model 1, plus age effects; Model 3: as in model 1, plus age square effects; Model 4: with additive, parity, permanent environmental, year and season effects; Model 5: as in model 4, plus age effects; Model 6: as in Model 4, plus age square effects; Model 7: with additive, parity, permanent environmental and year-month effects; Model 8: as in model 7, plus age effects; Model 9: as in model 7, plus age square; Model 10: with additive, parity, permanent environmental and year-season effects; Model 11: as in model 10, plus age effects; Model 12, as in model 10, plus age square effects; V_A, V_{Pe} and V_E are additive, permanent environmental, and residual variances, respectively; h^2 is narrow sense heritability (V_A/V_P); p^2 is the contribution of permanent environmental variance to phenotypic variance (V_{Pe}/V_P); e^2 is the contribution of residual variance to phenotypic variance (V_E/V_P); MSE: mean squared error; AIC: Akaike's information criterion.

6.3.2.2 Pannon White breed

Estimated additive genetic variances, permanent environmental and residual variances and ratios (compared to the phenotypic variance) are given in Tables 19-21 for all three litter size traits. Heritability estimates were low for NBA and TNB and close to zero for NBD. These estimates were in accordance with the heritability estimates of the relevant literature (Moura et al., 2001; García and Baselga, 2002a; García and Baselga, 2002b; Mantovani et al., 2008; Nagy et al., 2013b; Nagy et al., 2014). Although the different applied models did not result in substantially different heritability estimates, adding age or age-square (models 2, 3, 5, 6, 8, 9, 11, 12) they consistently reduced residual variance components of the examined traits. Several reasons could explain various heritabilites reported by the different studies, like genetic differences between the analysed rabbit breeds, observed environments and the different structures of the applied animal models. Nevertheless, most studies used only one model for genetic parameter estimation, therefore no tendency could be detected between the used model structure and the received heritability estimates. The estimates for the ratios of the permanent environmental variance to the phenotypic variance were low for NBD and moderate for NBA and TNB and they exceeded those of the additive genetic effects for NBA and TNB whereas the opposite was true for NBD. Our results were in the range of 0.03-0.18 for NBA; 0.01-0.07 for NBD and 0.07-0.13 for TNB as reported by the different authors (García and Baselga, 2002a; Garcia and Baselga, 2002b; Ragab et al., 2011; Nagy et al.

2011a; Nagy et al., 2013b; Nagy et al., 2014). Nevertheless, it must be emphasized that no clear propensity was reported in the literature about whether or not the ratios to the phenotypic variance of additive genetic was occupied the greater portion than that of the permanent environmental effects based on the estimated variance components for NBA, NBD and TNB.

The values characterizing the models' fit are provided in Tables 19-21. According to the MSE values of the observed and predicted litter size traits, models containing age or age-square showed a better goodness of fit than others. Bias values were practically zero for all traits and models. Statistically significant differences were found for NBA and TNB ($p<0.0001$) by comparing squared differences between the observed and predicted values based on the 12 models. On the contrary non-significant differences were observed for NBD ($p=0.8$). Based on the MSE estimating the goodness of fit for different models, model 8 was selected for NBA and TNB as the "best" model. For the sake of simplicity, model 8 was also chosen for NBD (where the fit was the same as that of model 9). Unfortunately, there was no similar evaluation available in the recent literature. However, Nagy et al. (2011b) also applied MSE of the observed and predicted NBA and TNB for comparing repeatability and multivariate models in the Pannon White and Ka rabbits, whose repeatability model had the same structure as model 8 of the present study.

Table 19. Estimated variance components, for number of kits born alive (NBA) of PW

Model	V_A	h^2	V_{Pe}	p^2	V_E	e^2	MSE	AIC
1	0.62 ± 0.02	0.07 ± 0.01	0.61 ± 0.02	0.07 ± 0.01	7.74 ± 0.02	0.86 ± 0.01	7.14	-24334
2	0.57 ± 0.02	0.07 ± 0.01	0.79 ± 0.02	0.09 ± 0.01	7.22 ± 0.02	0.84 ± 0.01	6.28	-22374
3	0.57 ± 0.02	0.07 ± 0.01	0.79 ± 0.02	0.09 ± 0.01	7.22 ± 0.02	0.84 ± 0.01	6.28	-22374
4	0.62 ± 0.02	0.07 ± 0.01	0.60 ± 0.02	0.07 ± 0.01	7.75 ± 0.02	0.86 ± 0.01	7.15	-24313
5	0.57 ± 0.02	0.07 ± 0.01	0.79 ± 0.02	0.09 ± 0.01	7.23 ± 0.02	0.84 ± 0.01	6.29	-22338
6	0.57 ± 0.02	0.07 ± 0.01	0.79 ± 0.02	0.09 ± 0.01	7.23 ± 0.02	0.84 ± 0.01	6.29	-22338
7	0.59 ± 0.02	0.07 ± 0.01	0.62 ± 0.02	0.07 ± 0.01	7.66 ± 0.02	0.86 ± 0.01	6.99	-24789
8	0.54 ± 0.02	0.06 ± 0.01	0.81 ± 0.02	0.10 ± 0.01	7.16 ± 0.02	0.84 ± 0.01	6.15	-22887
9	0.54 ± 0.02	0.06 ± 0.01	0.81 ± 0.02	0.10 ± 0.01	7.16 ± 0.02	0.84 ± 0.01	6.15	-22887
10	0.60 ± 0.02	0.07 ± 0.01	0.61 ± 0.02	0.07 ± 0.01	7.73 ± 0.02	0.86 ± 0.01	7.11	-24566
11	0.57 ± 0.02	0.07 ± 0.01	0.80 ± 0.02	0.09 ± 0.01	7.21 ± 0.02	0.84 ± 0.01	6.24	-22617
12	0.57 ± 0.02	0.07 ± 0.01	0.80 ± 0.02	0.09 ± 0.01	7.21 ± 0.02	0.84 ± 0.01	6.24	-22617

Model 1: with additive, parity, permanent environmental, year and month effects; Model 2: as in model 1, plus age effects; Model 3: as in model 1, plus age square effects; Model 4: with additive, parity, permanent environmental, year and season effects; Model 5: as in model 4, plus age effects; Model 6: as in Model 4, plus age square effects; Model 7: with additive, parity, permanent environmental and year-month effects; Model 8: as in model 7, plus age effects; Model 9: as in model 7, plus age square; Model 10: with additive, parity, permanent environmental and year-season effects; Model 11: as in model 10, plus age effects; Model 12, as in model 10, plus age square effects; V_A, V_{Pe} and V_E are additive, permanent environmental, and residual variances, respectively; h^2 is narrow sense heritability (V_A/V_P); p^2 is the contribution of permanent environmental variance to phenotypic variance (V_{Pe}/V_P); e^2 is the contribution of residual variance to phenotypic variance (V_E/V_P); MSE: mean squared error. AIC: Akaike's information criterion.

Table 20. Estimated variance components, for number of kits born dead (NBD) of PW

Model	V_A	h^2	V_{Pe}	p^2	V_E	e^2	MSE	AIC
1	0.023 ± 0.004	0.019 ± 0.004	0.014 ± 0.005	0.011 ± 0.004	1.166 ± 0.008	0.970 ± 0.004	1.14	-26796
2	0.024 ± 0.004	0.020 ± 0.003	0.011 ± 0.005	0.009 ± 0.004	1.172 ± 0.008	0.971 ± 0.004	1.09	-26939
3	0.024 ± 0.004	0.020 ± 0.003	0.011 ± 0.005	0.009 ± 0.004	1.172 ± 0.008	0.971 ± 0.004	1.09	-26939
4	0.023 ± 0.004	0.019 ± 0.004	0.013 ± 0.005	0.011 ± 0.004	1.169 ± 0.008	0.970 ± 0.004	1.14	-26799
5	0.024 ± 0.004	0.020 ± 0.003	0.010 ± 0.004	0.008 ± 0.004	1.174 ± 0.008	0.971 ± 0.004	1.09	-26938
6	0.024 ± 0.004	0.020 ± 0.003	0.010 ± 0.004	0.008 ± 0.004	1.174 ± 0.008	0.971 ± 0.004	1.09	-26938
7	0.022 ± 0.004	0.019 ± 0.004	0.015 ± 0.004	0.013 ± 0.004	1.146 ± 0.008	0.969 ± 0.004	1.10	-26911
8	0.023 ± 0.004	0.020 ± 0.004	0.012 ± 0.005	0.010 ± 0.004	1.151 ± 0.008	0.970 ± 0.004	1.06	-27039
9	0.023 ± 0.004	0.020 ± 0.004	0.012 ± 0.005	0.010 ± 0.004	1.151 ± 0.008	0.970 ± 0.004	1.06	-27039
10	0.023 ± 0.004	0.019 ± 0.004	0.013 ± 0.005	0.011 ± 0.004	1.161 ± 0.008	0.970 ± 0.004	1.13	-26884
11	0.024 ± 0.004	0.020 ± 0.004	0.010 ± 0.004	0.009 ± 0.004	1.167 ± 0.008	0.971 ± 0.003	1.08	-27039
12	0.024 ± 0.004	0.020 ± 0.004	0.010 ± 0.004	0.009 ± 0.004	1.167 ± 0.008	0.971 ± 0.003	1.08	-27039

Model 1: with additive, parity, permanent environmental, year and month effects; Model 2: as in model 1, plus age effects; Model 3: as in model 1, plus age square effects; Model 4: with additive, parity, permanent environmental, year and season effects; Model 5: as in model 4, plus age effects; Model 6: as in Model 4, plus age square effects; Model 7: with additive, parity, permanent environmental and year-month effects; Model 8: as in model 7, plus age effects; Model 9: as in model 7, plus age square; Model 10: with additive, parity, permanent environmental and year-season effects; Model 11: as in model 10, plus age effects; Model 12, as in model 10, plus age square effects; V_A, V_{Pe} and V_E are additive, permanent environmental, and residual variances, respectively; h^2 is narrow sense heritability (V_A/V_P); p^2 is the contribution of permanent environmental variance to phenotypic variance (V_{Pe}/V_P); e^2 is the contribution of residual variance to phenotypic variance (V_E/V_P); MSE: mean squared error. AIC: Akaike's information criterion.

Table 21. Estimated variance components, total number of born kits (TNB) of PW

Model	V_A	h^2	V_{Pe}	p^2	V_E	e^2	MSE	AIC
1	0.66 ± 0.02	0.07 ± 0.01	0.64 ± 0.02	0.07 ± 0.01	7.89 ± 0.02	0.86 ± 0.01	7.26	-26796
2	0.61 ± 0.02	0.07 ± 0.01	0.85 ± 0.02	0.10 ± 0.01	7.35 ± 0.02	0.84 ± 0.01	6.37	-26939
3	0.61 ± 0.02	0.07 ± 0.01	0.85 ± 0.02	0.10 ± 0.01	7.35 ± 0.02	0.84 ± 0.01	6.37	-26939
4	0.66 ± 0.02	0.07 ± 0.01	0.64 ± 0.02	0.07 ± 0.01	7.91 ± 0.02	0.86 ± 0.01	7.28	-26799
5	0.61 ± 0.02	0.07 ± 0.01	0.84 ± 0.02	0.10 ± 0.01	7.36 ± 0.02	0.83 ± 0.01	6.38	-26938
6	0.61 ± 0.02	0.07 ± 0.01	0.84 ± 0.02	0.10 ± 0.01	7.36 ± 0.02	0.83 ± 0.01	6.38	-26938
7	0.63 ± 0.02	0.07 ± 0.01	0.65 ± 0.02	0.07 ± 0.01	7.80 ± 0.02	0.86 ± 0.01	7.10	-26911
8	0.58 ± 0.02	0.07 ± 0.01	0.86 ± 0.02	0.10 ± 0.01	7.27 ± 0.02	0.83 ± 0.01	6.23	-27039
9	0.58 ± 0.02	0.07 ± 0.01	0.86 ± 0.02	0.10 ± 0.01	7.27 ± 0.02	0.83 ± 0.01	6.23	-27039
10	0.64 ± 0.02	0.07 ± 0.01	0.64 ± 0.02	0.07 ± 0.01	7.88 ± 0.02	0.86 ± 0.01	7.23	-26884
11	0.61 ± 0.02	0.07 ± 0.01	0.84 ± 0.02	0.10 ± 0.01	7.33 ± 0.02	0.83 ± 0.01	6.34	-27039
12	0.61 ± 0.02	0.07 ± 0.01	0.84 ± 0.02	0.10 ± 0.01	7.33 ± 0.02	0.83 ± 0.01	6.34	-27039

Model 1: with additive, parity, permanent environmental, year and month effects; Model 2: as in model 1, plus age effects; Model 3: as in model 1, plus age square effects; Model 4: with additive, parity, permanent environmental, year and season effects; Model 5: as in model 4, plus age effects; Model 6: as in Model 4, plus age square effects; Model 7: with additive, parity, permanent environmental and year-month effects; Model 8: as in model 7, plus age effects; Model 9: as in model 7, plus age square; Model 10: with additive, parity, permanent environmental and year-season effects; Model 11: as in model 10, plus age effects; Model 12, as in model 10, plus age square effects; V_A, V_{Pe} and V_E are additive, permanent environmental, and residual variances, respectively; h^2 is narrow sense heritability (V_A/V_P); p^2 is the contribution of permanent environmental variance to phenotypic variance (V_{Pe}/V_P); e^2 is the contribution of residual variance to phenotypic variance (V_E/V_P); MSE: mean squared error. AIC: Akaike's information criterion.

6.3.2.3 Pannon Ka breed

The variance genetic merit and their relative contributions compared to the phenotypic variance were presented in Tables 22-24 from different models for NBA, NBD and TNB. The various heritability estimates were low (<0.1). Although applied different models did not give considerably different heritability estimates, adding age or age-square (models 2, 3, 5, 6, 8, 9, 11, 12) slightly decreased residual variance components of NBA and TNB. The NBA, NBD and TNB heritability estimates in this study were comparable to the litter size traits estimates reported in relevant literatures (Rastogi et al., 2000, Moura et al., 2001;García and Baselga, 2002a, García and Baselga, 2002b; Piles et al., 2006, Mantovani et al., 2008; Nagy et al., 2013a). The variability among the heritability evaluations of these studies may result in genetic differences between the analysed rabbit breeds. Moreover, another reason of the different heritabilities can be related to the different structures of the applied animal models. Most of previous studies estimated the magnitude of genetic variances based on only one model. The ratios of the permanent environmental variance to the phenotypic variance were given in a low for NBD and moderate levels for NBA and TNB and they partly exceeded those of the additive genetic effects for the models adding age or age-square (models 2, 3, 5, 6, 8, 9, 11, 12). These estimates were similar levels given by other authors (García and Baselga, 2002a; Garcia and Baselga, 2002b; Ragab et al., 2011; Nagy et al., 2013a). Nevertheless, no clear tendency was found in literature to detect the different proportion of the phenotypic variance between the additive genetic and the permanent environmental effects.

Tests of the goodness of fit values for the used models of litter size traits are shown in Tables 22-24. Squared differences between the observed and predicted values of the 12 models were significant difference for NBA and TNB ($p<0.0001$), respectively but non-significant for NBD ($p=0.72$). It may be seen that the models containing age or age-square showed a better goodness of fit when compared to the other models because of the lower MSE values of the observed and predicted NBA, NBD and TNB. Bias values were practically zero for all traits and models. Therefore, model 8 was selected for NBA, NBD TNB as the “best” model based on the parameters evaluating the goodness of fit for different models which are the lowest for MSE and highest for correlation coefficients. Although no similar evaluation was found in the literature, Nagy et al. (2011b) applied MSE of the observed and predicted NBA and TNB compared repeatability and multivariate models and the repeatability model had the same structure as model 8 of the present study.

Table 22. Estimated variance components, for number of kits born alive (NBA) of PK

Model	V_A	h^2	V_{Pe}	p^2	V_E	e^2	MSE	AIC
1	0.83±0.03	0.09±0.01	0.62±0.02	0.07±0.01	7.68±0.02	0.84±0.01	7.01	-15194
2	0.59±0.03	0.07±0.01	0.93±0.03	0.11±0.01	6.98±0.02	0.82±0.01	6.01	-13040
3	0.59±0.03	0.07±0.01	0.93±0.03	0.11±0.01	6.98±0.02	0.82±0.01	6.01	-13040
4	0.81±0.03	0.09±0.01	0.64±0.02	0.07±0.01	7.71±0.02	0.84±0.01	7.04	-15203
5	0.57±0.03	0.07±0.01	0.94±0.02	0.11±0.01	6.99±0.02	0.82±0.01	6.03	-13027
6	0.57±0.03	0.07±0.01	0.94±0.02	0.11±0.01	6.99±0.02	0.82±0.01	6.03	-13027
7	0.73±0.03	0.08±0.01	0.68±0.02	0.08±0.01	7.58±0.02	0.84±0.01	6.84	-15338
8	0.57±0.03	0.07±0.01	0.93±0.02	0.11±0.01	6.89±0.02	0.82±0.01	5.86	-13182
9	0.57±0.03	0.07±0.01	0.93±0.02	0.11±0.01	6.89±0.02	0.82±0.01	5.86	-13182
10	0.75±0.03	0.08±0.01	0.67±0.02	0.07±0.01	7.66±0.02	0.84±0.01	6.97	-15270
11	0.56±0.03	0.07±0.01	0.92±0.02	0.11±0.01	6.98±0.02	0.82±0.01	6.00	-13150
12	0.56±0.03	0.07±0.01	0.92±0.02	0.11±0.01	6.98±0.02	0.82±0.01	6.00	-13150

Model 1: with additive, parity, permanent environmental, year and month effects; Model 2: as in model 1, plus age effects; Model 3: as in model 1, plus age square effects; Model 4: with additive, parity, permanent environmental, year and season effects; Model 5: as in model 4, plus age effects; Model 6: as in Model 4, plus age square effects; Model 7: with additive, parity, permanent environmental and year-month effects; Model 8: as in model 7, plus age effects; Model 9: as in model 7, plus age square; Model 10: with additive, parity, permanent environmental and year-season effects; Model 11: as in model 10, plus age effects; Model 12, as in model 10, plus age square effects; V_A, V_{Pe} and V_E are additive, permanent environmental, and residual variance, respectively; h^2 is narrow sense heritability (V_A/V_P); p^2 is the contribution of permanent environmental variance to phenotypic variance (V_{Pe}/V_P); e^2 is the contribution of residual variance to phenotypic variance (V_E/V_P); MSE: mean squared error. AIC: Akaike's information criterion.

Table 23. Estimated variance components, for number of kits born dead (NBD) of PK

Model	V_A	h^2	V_{Pe}	p^2	V_E	e^2	MSE	AIC
1	0.12±0.01	0.03±0.01	0.09±0.01	0.02±0.01	3.47±0.02	0.94±0.01	3.32	-20458
2	0.11±0.01	0.03±0.01	0.10±0.01	0.03±0.01	3.43±0.02	0.94±0.01	3.14	-19954
3	0.11±0.01	0.03±0.01	0.10±0.01	0.03±0.01	3.43±0.02	0.94±0.01	3.14	-19954
4	0.12±0.01	0.03±0.01	0.09±0.01	0.03±0.01	3.47±0.02	0.94±0.01	3.33	-20403
5	0.11±0.01	0.03±0.01	0.10±0.01	0.03±0.01	3.43±0.02	0.94±0.01	3.14	-19892
6	0.11±0.01	0.03±0.01	0.10±0.01	0.03±0.01	3.43±0.02	0.94±0.01	3.14	-19892
7	0.10±0.01	0.03±0.01	0.10±0.01	0.03±0.01	3.44±0.02	0.95±0.01	3.27	-20700
8	0.09±0.01	0.03±0.01	0.11±0.01	0.03±0.01	3.40±0.02	0.94±0.01	3.08	-20163
9	0.09±0.01	0.03±0.01	0.11±0.01	0.03±0.01	3.40±0.02	0.94±0.01	3.08	-20163
10	0.11±0.01	0.03±0.01	0.10±0.01	0.03±0.01	3.47±0.02	0.94±0.01	3.31	-20584
11	0.10±0.01	0.03±0.01	0.11±0.01	0.03±0.01	3.42±0.02	0.94±0.01	3.13	-20054
12	0.10±0.01	0.03±0.01	0.11±0.01	0.03±0.01	3.42±0.02	0.94±0.01	3.13	-20054

Model 1: with additive, parity, permanent environmental, year and month effects; Model 2: like model 1, plus age effects; Model 3: like in model 1, plus age square effects ; Model 4: with additive, parity, permanent environmental, year and season effects; Model 5: like model 4, plus age effects; Model 6: like Model 4, plus age square effects; Model 7: with additive, parity, permanent environmental and year-month effects; Model 8: like model 7, plus age effects; Model 9: like in model 7, plus age square; Model 10: with additive, parity, permanent environmental and year-season effects; Model 11: like model 10, plus age effects; Model 12, like in model 10, plus age square effects; V_A, V_{Pe} and V_E are additive, permanent environmental, and residual variances, respectively; h^2 is narrow sense heritability (V_A/V_P); p^2 is the contribution of permanent environmental variance to phenotypic variance (VPe/VP); e^2 is the contribution of residual variance to phenotypic variance (V_E/V_P); MSE: mean squared error. AIC: Akaike's information criterion.

Table 24. Estimated variance components, total number of born kits (TNB) of PK

Model	V_A	h^2	V_{Pe}	p^2	V_E	e^2	MSE	AIC
1	1.00±0.03	0.10±0.01	0.68±0.02	0.07±0.01	8.16±0.02	0.83±0.01	7.41	-15926
2	0.71±0.03	0.08±0.01	1.02±0.03	0.11±0.01	7.34±0.02	0.81±0.01	6.31	-13551
3	0.71±0.03	0.08±0.01	1.02±0.03	0.11±0.01	7.34±0.02	0.81±0.01	6.31	-13551
4	0.97±0.03	0.10±0.01	0.68±0.02	0.07±0.01	8.16±0.02	0.83±0.01	7.44	-15949
5	0.67±0.03	0.07±0.01	1.05±0.03	0.12±0.01	7.36±0.02	0.81±0.01	6.33	-13547
6	0.67±0.03	0.07±0.01	1.05±0.03	0.12±0.01	7.36±0.02	0.81±0.01	6.33	-13547
7	0.87±0.03	0.09±0.01	0.71±0.02	0.07±0.01	8.02±0.02	0.84±0.01	7.23	-16020
8	0.68±0.03	0.08±0.01	1.02±0.03	0.11±0.01	7.23±0.02	0.81±0.01	6.14	-13625
9	0.68±0.03	0.08±0.01	1.02±0.03	0.11±0.01	7.23±0.02	0.81±0.01	6.14	-13625
10	0.92±0.03	0.09±0.01	0.69±0.02	0.07±0.01	8.10±0.02	0.83±0.01	7.37	-15962
11	0.68±0.03	0.08±0.01	1.01±0.03	0.11±0.01	7.33±0.02	0.81±0.01	6.29	-13630
12	0.68±0.03	0.08±0.01	1.01±0.03	0.11±0.01	7.33±0.02	0.81±0.01	6.29	-13630

Model 1: with additive, parity, permanent environmental, year and month effects; Model 2: as in model 1, plus age effects; Model 3: as in model 1, plus age square effects; Model 4: with additive, parity, permanent environmental, year and season effects; Model 5: as in model 4, plus age effects; Model 6: as in Model 4, plus age square effects; Model 7: with additive, parity, permanent environmental and year-month effects; Model 8: as in model 7, plus age effects; Model 9: as in model 7, plus age square; Model 10: with additive, parity, permanent environmental and year-season effects; Model 11: as in model 10, plus age effects; Model 12, as in model 10, plus age square effects; V_A, V_{Pe} and V_E are additive, permanent environmental, and residual variances, respectively; h^2 is narrow sense heritability (V_A/V_P); p^2 is the contribution of permanent environmental variance to phenotypic variance (V_{Pe}/V_P); e^2 is the contribution of residual variance to phenotypic variance (V_E/V_P); MSE: mean squared error. AIC: Akaike's information criterion.

6.3.3 Non-additive models

6.3.3.1 Pannon Large breed

After determining the best fitted models for every trait they were extended with dominance effects. The variance component estimates and their relative contributions to the total phenotypic variance for NBA, NBD and TNB are presented in Table 25. When comparing the estimated variance components of NBA, NBD and TNB in Table 25 and those of model 8 in Tables 16-18 it may be seen that the estimated additive genetic variances decreased for NBA and for TNB, while the permanent environmental variance substantially decreased for all examined traits for the extended models (containing dominance effects). This phenomenon is called confounding and because the litter effect is highly confounded with family (Vitezica et al., 2013) it is often observed to be connected to dominance models in prolific species such as chickens and pigs. Confounding between dominance and common litter effects in swine and poultry was observed in several studies summarized by Nagy et al. (2013b). However, as it was mentioned by Nagy et al. (2013b), it is generally assumed that common litter effects are negligible for litter size composite traits. Consequently, according to the relevant literature this effect is not used when genetic parameters are estimated. In similar studies confounding between the additive genetic dominance and permanent environmental effects was reported by Nagy et al. (2013b and 2014) for the Pannon White

and Pannon Ka rabbit breeds; however, the magnitude of the phenomenon was much smaller than in the present study. In contrast to a study by Nagy et al. (2013b and 2014), where the magnitudes of the additive genetic and the dominance variances were similar, in the present study the ratio of dominance variance to phenotypic substantially exceeded the heritability estimates for all examined traits. As it was mentioned by Toro and Varona (2010), one of the reasons that dominance effects are often neglected is that due to the computational complexity this variance component requires larger datasets when compared to conventional animal models. The possibility of overestimating the additive genetic variance with models that ignore dominance effect was demonstrated by Norris et al. (2002) in a simulation study, where the overestimation of the additive genetic variance with reduced models (not containing the dominance effects) was proportional with the increasing proportion of full-sibs and also with the increasing magnitude of dominance effects.

Table 25. Estimated variance components and variance ratios based on extended models for the number of kits born alive (NBA), number of kits born dead (NBD) and total number of kits born (TNB) of PL

Traits	**V_A**	**h^2**	**V_{Pe}**	**p^2**	**V_D**	**d^2**	**V_E**	**e^2**
NBA	0.52 ± 0.26	0.06 ± 0.0283	0.87 ± 0.29	0.09 ± 0.0310	2.52 ± 0.85	0.27 ± 0.024	5.29 ± 0.17	0.58 ± 0.02
NBD	0.09 ± 0.07	0.02 ± 0.0125	0.25 ± 0.12	0.05 ± 0.0237	0.24 ± 0.25	0.05 ± 0.013	4.74 ± 0.10	0.89 ± 0.02
TNB	0.19 ± 0.22	0.02 ± 0.0202	0.69 ± 0.29	0.07 ± 0.0277	3.84 ± 0.87	0.38 ± 0.025	5.35 ± 0.17	0.53 ± 0.02

V_A, V_{Pe} V_D, and V_E are additive, dominance, permanent environmental and residual variances, respectively; h^2 is narrow sense heritability (V_A/V_P); p^2 is the contribution of permanent environmental variance to phenotypic variance (V_{Pe}/V_P); d^2 is the contribution of dominance variance to phenotypic variance (V_D/V_P); e^2 is the contribution of residual variance to phenotypic variance (V_E/V_P)

6.3.3.2 Pannon White breed

Three selected models for litter size traits as the best fitted models were extended with dominance effects. Estimates of variance components relative to the phenotypic variance for additive genetic, permanent environment, dominance effects and residual of NBA, NBD and TNB are presented in Table 26. It can be seen that the values of the additive genetic and permanent environmental variances of analysed traits considerably decreased comparing to model 8 in Tables 19-21. These reductions signalled confounding between dominance and those mentioned effects for all litter traits. Vitezica et al. (2013) also reported that the litter effects are highly confounded with family in prolific species. The current trends of confounding were similar to that of previous studies (Nagy et al. 2013b and 2014). It was argued that ignoring to calculate dominance effect from animal models resulted from the technical and computational difficulties faced to analyse large dataset in herds (Toro and Varona 2010).

Table 26. Estimated variance components and variance ratios based on the extended models for number of kits born alive (NBA), number of kits born dead (NBD) and total number of kits born (TNB) of PW

Traits	**V_A**	**h^2**	**V_{Pe}**	**p^2**	**V_D**	**d^2**	**V_E**	**e^2**
NBA	0.49±0.09	0.06±0.01	0.64±0.10	0.08±0.01	0.19±0.27	0.09±0.01	7.15±0.07	0.84±0.01
NBD	0.02±0.01	0.02±0.01	0.009±0.005	0.008±0.005	0.003±0.009	0.01±0.002	1.15±0.01	0.97±0.01
TNB	0.53±0.09	0.06±0.01	0.70± 0.11	0.08±0.01	0.17±0.27	0.08±0.01	7.27±0.08	0.84±0.01

V_A, V_{Pe} V_D, and V_E are additive, dominance, permanent environmental, and residual variances, respectively; h^2 is narrow sense heritability (V_A/V_P); p^2 is the contribution of permanent environmental variance to phenotypic variance (V_{Pe}/V_P); d^2 is the contribution of dominance variance to phenotypic variance (V_D/V_P); e^2 is the contribution of residual variance to phenotypic variance (V_E/V_P);

6.3.3.3 Pannon Ka breed

The best chosen fitted models for each trait were extended with dominance effects. The magnitude and ratios (compared to the phenotypic variance) of additive genetic, permanent environmental and residual variance components for NBA, NBD and TNB are presented in Table 27. The lower values of the estimated variance components and the permanent environmental variance of NBA and NBD for the extended models (containing dominance effects) in Table 27 were found in compared with those of model 8 in Tables 22-24. This phenomenon is called confounding because the litter effect is highly confounded with family (Vitezica et al., 2013) and especially, in prolific species such as chickens, pigs and rabbits, the litter effect is highly confounded with family (Esfandyari et al., 2016). Nagy et al., (2013b) was resumed that confounding between dominance and common litter effects in swine and poultry was observed in several studies and common litter effects are negligible for litter size composite traits. Thus, this effect was ignored in estimated genetic parameters. The smaller magnitude phenomenon between the additive genetic dominance and permanent environmental effects also was reported by Nagy et al. (2013b and 2014) for the Pannon White and Pannon Ka rabbit breeds compared with the present study. The exceeded ratio of dominance variance to phenotypic compared with the heritability estimates for NBA, NBD and TNB (noted that the standard error of TNB is high) meanwhile those ratios had similar values in previous studies (Nagy et al., 2013b, Nagy et al., 2014). Norris et al. (2002) presented that overestimated additive genetic variance could be calculated with models ignoring dominance effect and the more rising proportion of full-sibs, the more increasing magnitude of dominance effects.

Table 27. Estimated variance components and variance ratios based on the extended models for number of kits born alive (NBA), number of kits born dead (NBD) and total number of kits born (TNB) of PK

Traits	**V_A**	**h^2**	**V_{Pe}**	**p^2**	**V_D**	**d^2**	**V_E**	**e^2**
NBA	0.47±0.11	0.06±0.01	0.67±0.11	0.08±0.01	0.33±0.32	0.16±0.01	6.88±0.09	0.82±0.01
NBD	0.06±0.03	0.02±0.01	0.04±0.04	0.01±0.01	0.10±0.10	0.10±0.01	3.40±0.04	0.95±0.01
TNB	0.57±6.98	0.06±0.80	0.76±8.09	0.09±0.87	0.34±21.08	0.15±0.69	7.23±24.93	0.81±1.21

V_A, V_{Pe}, V_D, and V_E are additive, dominance, permanent environmental, and residual variances, respectively; h^2 is narrow sense heritability (V_A/V_P); p^2 is the contribution of permanent environmental variance to phenotypic variance (V_{Pe}/V_P); d^2 is the contribution of dominance variance to phenotypic variance (V_D/V_P); e^2 is the contribution of residual variance to phenotypic variance (V_E/V_P)

6.4 Genetic trends

6.4.1 Pannon Large breed

6.4.1.1 Genetic trends of additive effects models

When comparing the estimated genetic trends for the analysed traits (Tables 28) it could be seen that they became significantly lower for the models containing age or age-square. Calculated mean genetic trends for the applied 12 models were 0.05 for NBA, closer to 0 for NBD and 0.03 for TNB, respectively. The values received for NBA are favourable, because the Pannon Large rabbit breed was never selected for litter size composite traits. The obtained average genetic trend for NBA was higher than the reported value (0.03) for the Botucatu rabbit, which is a multi-purpose line (Moura et al., 2001). Nevertheless, the genetic trends reported in the present study were lower than those obtained by other researchers (Garreau et al. 2005); García and Baselga 2002a; García and Baselga 2002b; Lenoir and Garreau 2009). These authors estimated an annual genetic trend of 0.11- 0.21 kits per year for TNB and 0.11-0.23 kits per year for NBA using reproductive performance records of Spanish and French maternal rabbit breeds (selected for reproductive traits). However, the direct response to selection may also be determined using embryo cryopreservation (García and Baselga 2002a; García and Baselga 2002b). At thawing of embryos the selection response was obtained for the Spanish V line (selected for litter size at weaning) between the 15^{th} and 21^{st} and between the 17^{th} and 26^{th} generations. The annual genetic trends were also estimated using the BLUP methodology. García and Baselga (2002a) observed a very good agreement between the results based on the two methods (when converted to the annual trend they were 0.14 vs 0.15 for TNB and 0.13 vs 0.15 for NBA). In contrast, values reported by García and Baselga (2002b) were much less consistent (0.11 vs 0.21 for TNB and 0.11 vs 0.23 for NBA). As it was noted by the authors, a possible explanation for this difference may be provided by the fact that the applied BLUP model contained no dominance effects, thus heritability of these traits could be overestimated.

Table 28. Estimated genetic trends and parameters evaluating the goodness of fit for models for the number of kits born alive (NBA), kits born dead (NBD) and total number of born kits (TNB) of PL

Model	Genetic trend		
	NBA	NBD	TNB
1	$0.081^{a} \pm 0.005$	$-0.0019^{c} \pm 0.0007$	$0.061^{e} \pm 0.003$
2	$0.042^{b} \pm 0.006$	$-0.0021^{d} \pm 0.00059$	$0.024^{f} \pm 0.004$
3	$0.042^{b} \pm 0.006$	$-0.0021^{d} \pm 0.00059$	$0.024^{f} \pm 0.004$
4	$0.075^{a} \pm 0.005$	$-0.0015^{c} \pm 0.00077$	$0.059^{e} \pm 0.003$
5	$0.043^{b} \pm 0.006$	$-0.0018^{d} \pm 0.00066$	$0.027^{f} \pm 0.004$
6	$0.043^{b} \pm 0.006$	$-0.0018^{d} \pm 0.00066$	$0.027^{f} \pm 0.004$
7	$0.074^{a} \pm 0.004$	$0.0049^{c} \pm 0.0009$	$0.049^{e} \pm 0.002$
8	$0.035^{b} \pm 0.005$	$-0.0017^{d} \pm 0.00045$	$0.016^{f} \pm 0.003$
9	$0.035^{b} \pm 0.005$	$-0.0017^{d} \pm 0.0004$	$0.016^{f} \pm 0.003$
10	$0.083^{a} \pm 0.004$	$0.0055^{c} \pm 0.00101$	$0.064^{e} \pm 0.003$
11	$0.040^{b} \pm 0.006$	$-0.0023^{d} \pm 0.00064$	$0.023^{f} \pm 0.003$
12	$0.040^{b} \pm 0.006$	$-0.0021^{d} \pm 0.00069$	$0.023^{f} \pm 0.003$

[a, b, c, d, e, f] Estimated genetic trends with different letters (superscripts) were significantly different for NBA, NBD and TNB.

6.4.1.2 Genetic trends of non-additive effects models

Due to the decreased additive genetic variances of the extended models the annual genetic trends (0.03, -0.003 and 0.01) of NBA, NBD and TNB were also decreased when compared to the estimates of model 8 (Tables 16-18). The direct consequence of ignoring dominance effects from the animal models may probably be best evaluated by comparing the estimated breeding values predicted with the best fitted model (model 8) and with the same model extended with dominance effects.

6.4.2 Pannon White breed

6.4.2.1 Genetic trends of additive effects models

Genetic trends can be seen in Table 29. Based on the results the genetic trends were significantly lower for the models containing age or age-square of NBA and TNB whereas that of NBD presented an opposite trend. Mean of these trends were 0.03 for NBA, closer to 0 for NBD and 0.04 for TNB, respectively, for the applied 12 models. It can be noted that the studied breed was never selected for litter size composite traits. Furthermore, the obtained average genetic trend for NBA was higher than the reported value (0.001) for the Egyptian line (Hanaa et al., 2014) and was similar to those observed by Moura et al., 2001 for multi-purpose line. Nevertheless, the obtained trend of the PW breed was lower than those reported by several other studies (Garreau et al. 2005); García and Baselga 2002a; García and Baselga

2002b; Lenoir and Garreau 2009) where the annual genetic trends were 0.11-0.21 kits for TNB and 0.11-0.23 kits for NBA.

Table 29. Estimated genetic trends and parameters evaluating the goodness of fit for models for the number of kits born alive (NBA), kits born dead (NBD) and total number of born kits (TNB) of PW

Model	Genetic trend		
	NBA	NBD	TNB
1	$0.036^{a} \pm 0.004$	$-0.00002^{d} \pm 0.0003$	$0.0487^{m} \pm 0.004$
2	$0.029^{b} \pm 0.003$	$-0.00004^{e} \pm 0.0003$	$0.0262^{n} \pm 0.004$
3	$0.029^{b} \pm 0.003$	$-0.00004^{e} \pm 0.0003$	$0.0262^{n} \pm 0.004$
4	$0.033^{a} \pm 0.004$	$-0.00003^{d} \pm 0.0003$	$0.0471^{m} \pm 0.004$
5	$0.028^{b} \pm 0.003$	$0.00001^{e} \pm 0.0003$	$0.0259^{n} \pm 0.004$
6	$0.028^{b} \pm 0.003$	$0.00001^{e} \pm 0.0003$	$0.0259^{n} \pm 0.004$
7	$0.049^{c} \pm 0.004$	$0.00014^{e} \pm 0.0003$	$0.0486^{m} \pm 0.004$
8	$0.027^{b} \pm 0.004$	$0.00034^{f} \pm 0.0002$	$0.0258^{n} \pm 0.004$
9	$0.027^{b} \pm 0.004$	$0.00034^{f} \pm 0.0002$	$0.0258^{n} \pm 0.004$
10	$0.050^{c} \pm 0.004$	$0.00007^{dfh} \pm 0.0003$	$0.0499^{m} \pm 0.004$
11	$0.029^{b} \pm 0.004$	$0.00019^{e} \pm 0.0003$	$0.0283^{n} \pm 0.004$
12	$0.029^{b} \pm 0.004$	$0.00019^{e} \pm 0.0003$	$0.0283^{n} \pm 0.004$

[a, b, c, d, e, f, h, m, n] Estimated genetic trends with different letters (superscripts) were significantly different for NBA, NBD and TNB.

6.4.2.2 Genetic trends of non-additive effects models

Due to the slightly decreased additive genetic variances of the extended models, the annual genetic trends (0.026, -0.0004 and 0.0255) of NBA, NBD and TNB declined compared to the estimates of model 8 (Tables 19-21).

6.4.3 Pannon Ka breed

6.4.3.1 Genetic trends of additive effects models

Tables 30 showed the significantly lower genetic trends for the analysed traits of the models containing age or age-square. Mean of genetic trends for the applied 12 models were calculated 0.08 for NBA, closer to 0 for NBD and 0.09 for TNB, respectively. These results are favourable since the Pannon Ka rabbit breed was selected for litter size composite traits. The higher average genetic trend was received in compared to the reported values such as 0.03 for NBA of multi-purpose line (Moura et al., 2001) and 0.001 for NBA and 0.002 for TNB of synthetic maternal line (Hanaa et al., 2014). Nevertheless, the slightly lower of genetic trends in the present study were found compared to other researchers (García and Baselga 2002a; García and Baselga 2002b) using Spanish maternal rabbit breeds selected for reproductive traits.

Table 30. Estimated genetic trends and parameters evaluating the goodness of fit for models for the number of kits born alive (NBA), kits born dead (NBD) and total number of born kits (TNB) of PK

Model	Genetic trend		
	NBA	NBD	TNB
1	0.13^{a}±0.01	-0.0004^{c}±0.0008	0.15^{e}±0.01
2	0.06^{b}±0.01	-0.0030^{d}±0.0010	0.07^{f}±0.01
3	0.06^{b}±0.01	-0.0030^{d}±0.0010	0.07^{f}±0.01
4	0.12^{a}±0.01	-0.0016^{d}±0.0008	0.14^{e}±0.01
5	0.06^{b}±0.01	-0.0039^{d}±0.0010	0.07^{f}±0.01
6	0.06^{b}±0.01	-0.0039^{d}±0.0010	0.07^{f}±0.01
7	0.11^{a}±0.01	0.0002^{c}±0.0005	0.13^{e}±0.01
8	0.06^{b}±0.01	-0.0016^{d}±0.0006	0.07^{f}±0.01
9	0.06^{b}±0.01	-0.0016^{d}±0.0006	0.07^{f}±0.01
10	0.11^{a}±0.01	-0.0005^{c}±0.0006	0.13^{e}±0.01
11	0.06^{b}±0.01	-0.0030^{d}±0.0009	0.07^{f}±0.01
12	0.06^{b}±0.01	-0.0030^{d}±0.0009	0.07^{f}±0.01

[a, b, c, d, e, f] Estimated genetic trends with different letters (superscripts) were significantly different for NBA, NBD and TNB.

6.4.3.2 Genetic trends of non-additive effects models

Following the dropped additive genetic variances of the extended models, the genetic trends per year (0.05, -0.001 and 0.06) of NBA, NBD and TNB, respectively, were decreased compared to the estimates of model 8 (Tables 22-24).

6.5 Stability of breeding values

6.5.1 Pannon Large breed

Estimated breeding values (with and without dominance effects) of NBA, NBD and TNB showed high rank correlation coefficients (0.98, 0.96 and 0.97), respectively. When the best 100 does were selected according to the different model types, the number of animals included jointly in the models was 80, 86 and 80. According to Nagy et al. (2013b and 2014), single trait models showed high breeding value stability, but even in this case some re-ranking may occur among the top ranked animals. In contrast, Nagy et al. (2014) observed a much lower concordance among breeding values when NBA and NBD were evaluated based on bivariate models. In the analyzed rabbit population the dominance components exceeded the additive genetic variance components for NBA, NBD and TNB, thus inclusion of dominance effects in the model was justified. In this study neglecting dominance effects resulted in an overestimation of additive genetic variances and genetic trends and due to the re-ranking certain differences were found among rabbits selected as top ranked animals.

However, it has to be kept in mind that precise estimation of dominance effects requires a relatively large dataset and a high proportion of full-sibs.

6.5.2 Pannon White breed

Based on estimated breeding values (with and without dominance effects) of NBA, NBD and TNB, their correlation coefficients are around 0.99 for all traits in Figures 5-7 which is very high rank and there are 94 animals in common by selecting 100 best animal based on those models. Although single trait models presented high breeding value stability, some re-ranking may occur among the top ranked animals (Nagy et al. 2013b and 2014).

6.5.3 Pannon Ka breed

It can be seen that the direct consequence of ignoring dominance effects from the animal models had a slight bias estimated breeding values with rank correlation coefficients (0.99, 0.98 and 0.99) in Figures 8-10, respectively, based on compared the best fitted model (model 8) with the extended model with dominance effects for each trait. When the best 100 does were selected according to the different model types, the number of animals included jointly in the models was 93, 89 and 91. The current results were comparable with other studies (Nagy et al., 2013b; Nagy et al., 2014) which showed some re-ranking may occur among the top ranked animals with high breeding value stability.

7. Conclusions and suggestions

Based on the results the following conclusions can be drawn.

1. In three Pannon rabbit breeds (Pannon Ka, Pannon Large and Pannon White) the contribution of cytoplasmic and D-loop mtDNA sequence effects on litter size have been estimated. This type of analyses has been performed in rabbit populations for the first time. The observed effects of both estimates, coming from cytoplasmic or D-loop mtDNA variation, were negligible.

2. Diversity of genetic parameters were shown based on comparing 12 models with different fix effects and the structures of the "best" models contain parity, age of the doe and year-month of kindling effects for three Pannon rabbit breeds.

3. In the Pannon rabbit breeds' population, heritability estimates were low for all traits. The ratios of the permanent environmental and the phenotypic variances exceeded of the heritability estimates for PL whereas that of ratios were showed the different levels with those heritabilities for PW and PK.

4. Extended models with dominance effects on litter size traits, heritability, permanent environmental effects estimates and genetics trends decreased for all breeds. Ratios of the dominance effects exceeded those of the heritability estimates for all breeds. On the contrary for NBD (PW) ratio of the dominance effects was smaller than the heritability estimates. Thus inclusion of dominance effects in the model was justified.

5. In these studies neglecting dominance effects resulted in an overestimation of additive genetic variances and genetic trends because some confounding with additive genetic and with permanent environmental effects were found. Spearman rank correlation coefficients between breeding values of the additive and dominance models were high 0.96-0.99 for all traits and all breeds and the re-ranking certain differences were found among rabbits selected as top ranked animals.

Based on the numerous studies it can be concluded that dominance effects are important due to some above mentioned changes and should be included in animal models of breeding value estimation. Neglecting dominance effects results in confounding that is the dominance effects will appear in other random effects such as additive genetic effects or permanent environmental effects thus breeding value estimation becomes less precise. However it has to

be kept in mind that precise estimation of dominance effect requires large datasets, large number of full sibs and time consuming process. Moreover, the magnitude of potential benefits of the introduction or alteration of mitogenome variation in the rabbit breeding remains an open question for future research.

8. New scientific results

1. The structures of the “best” models contain parity, age of the doe and year-month of kindling effects for three Pannon rabbit breeds to estimate the genetic parameters, predict the breeding values for litter size traits.

2. Heritability estimates were low for all traits and ranged between 0.07-0.08± 0.018-0.021 for NBA, 0.01-0.02± 0.009 for NBD and 0.04-0.05± 0.015-0.018 for TNB of Pannon Large rabbits; ranged between 0.06-0.07±0.01 for NBA, 0.019-0.020±0.003-0.004 for NBD and 0.07±0.01 for TNB of Pannon White rabbits; ranged between 0.07-0.09±0.01 for NBA, 0.03±0.01 for NBD and 0.07-0.10±0.01 for TNB of Pannon Ka rabbits.

3. Ratios of dominance to phenotypic variance were 0.27 ± 0.024 for NBA, 0.05 ± 0.013 for NBD and 0.38 ± 0.025 for TNB of Pannon Large rabbits; 0.09 ± 0.01 for NBA, 0.01 ± 0.002 for NBD and 0.08 ± 0.01 for TNB of Pannon White rabbits; 0.16 ±0.01 for NBA, 0.1 ± 0.01 for NBD and 0.15 ± 0.69 for TNB of Pannon Ka rabbits.

4. The predicted genetics trends with and without dominance effects were low (0.035 vs 0.03, -0.0017 vs -0.003 and 0.016 vs 0.01 for NBA, NBD and TNB, respectively) of Pannon Large rabbits; (0.027 vs 0.026, 0.0003 vs -0.0004 and 0.0258 vs 0.0255 for NBA, NBD and TNB, respectively) of Pannon White rabbits; (0.05 vs 0.06, -0.001 vs -0.0016 and 0.06 vs 0.07 for NBA, NBD and TNB, respectively) of Pannon Ka rabbits. Spearman rank correlation coefficients between breeding values of the additive and dominance models were high for all traits (0.96-0.99) and breeds.

9. Summary

Although, with controversial results, the effects of the mitogenome variation on economically important traits have been are reported in a number of domestic animal species. Here, in three Pannon rabbit breeds (Pannon Ka, Pannon Large and Pannon White) we have estimated the contribution of cytoplasmic and D-loop mtDNA sequence effects on litter size traits. This type of analyses has been performed in rabbit populations for the first time. The observed effects of both estimates, coming from cytoplasmic or D-loop mtDNA variation, were negligible. The lack of complete mitogenome polymorphism, as suggested from the analysis performed on the D-loop mtDNA sequence, is the most likely explanation for the observed results.

Genetic parameters and genetic trends for the number of kits born alive (NBA), number of kits born dead (NBD) and the total number of born kits were estimated in 6269 kindling records (collected between 2004-2015) of 1469 Pannon Large does inseminated with the sperm of 686 bucks; 21060 kindling records (collected between 1992-2016) of 4926 Pannon White (PW) does inseminated with the sperm of 1414 PW; 15833 kindling records (collected between 1999-2016) of 3691 PK does inseminated with the sperm of 1096 PK bucks. Using the REML method 12 single trait models were examined.

Heritability estimates were low for all traits and ranged between 0.07-0.08± 0.018-0.021 for NBA, 0.01-0.02± 0.009 for NBD and 0.04-0.05± 0.015-0.018 for TNB of PL; ranged between 0.06-0.07±0.01 for NBA, 0.019-0.020±0.003-0.004 for NBD and 0.07±0.01 for TNB of PW; ranged between 0.07-0.09±0.01 for NBA, 0.03±0.01 for NBD and 0.07-0.10±0.01 for TNB of PK.

The ratios of the permanent environmental variances exceeded of the heritability estimates and ranged between 0.11-0.16±0.016-0.018 for NBA, 0.06-0.07 ±0.014-0.015 for NBD and 0.11-0.17±0.014-0.017 for TNB of PL; ranged between 0.07-0.09±0.01 for NBA, 0.06-0.07±0.008-0.013 for NBD and 0.07-0.10±0.01 for TNB of PW; ranged between 0.07-0.11±0.01 for NBA, 0.02-0.03±0.01 for NBD and 0.07-0.11±0.01 for TNB of PK.

When characterizing the goodness of models bias values were practically zero for all traits, models and all breeds. After identifying the best fitted model (containing parity, age of the doe and year-month of kindling effects) it was extended with dominance effects for all breeds.

As a result, heritability estimates decreased to 0.06 ± 0.028 for NBA, 0.02 ±0.012 for NBD and 0.02± 0.022 for TNB of PW; 0.06±0.01 for NBA, 0.02±0.01 for NBD and 0.06±0.01 for TNB of PW; 0.06±0.01 for NBA, 0.02±0.01 for NBD and 0.06±0.80for TNB of PK.

The relative importance of the permanent environmental effects also decreased to 0.09±0.031 for NBA, 0.05±0.024 for NBD and 0.07±0.028 for TNB of PL; 0.08±0.01 for NBA, 0.008±0.005 for NBD and 0.08±0.001 for TNB of PW; 0.08±0.01 for NBA, 0.01 ± 0.01 for NBD and 0.09 ± 0.87for TNB of PK.

Ratios of the dominance effects exceeded those of the heritability estimates and amounted to 0.27 ±0.024 for NBA, 0.05 ±0.013 for NBD and 0.38±0.025 for TNB of PL; 0.09 ± 0.01for NBA and 0.08±0.01 for TNB of PW; 0.16±0.01 for NBA,0.1±0.01 for NBD and 0.15± 0.69 for TNB of PK.

On the contrary for NBD (PW) ratio of the dominance effects was smaller than the heritability estimates 0.01±0.002.

When compared to the additive model, the model including dominance showed some confounding with additive genetic and with permanent environmental effects and reduced calculated genetics trends (0.035 vs 0.03, -0.0017 vs -0.003 and 0.016 vs 0.01 for NBA, NBD and TNB, respectively) of PL; (0.027 vs 0.026, 0.0003 vs -0.0004 and 0.0258 vs 0.0255 for NBA, NBD and TNB, respectively) of PW; (0.05 vs 0.06, -0.001 vs -0.0016 and 0.06 vs 0.07 for NBA, NBD and TNB, respectively) of PK.

Spearman rank correlation coefficients between breeding values of the additive and dominance models were high for all traits (0.96-0.98) of PL; (0.99) of PW; (0.98-0.99) of PK. When dominance effects were included some re-ranking was observed among the top ranked animals for every trait.

10. Összefoglalás

A mitogenom variabilitás hatását eddig számos domesztikált állatfaj értékmérő tulajdonságára vizsgálták, bár a kapott eredmények ellentmondásosak voltak. A doktori disszertáció keretében a Pannon nyúltenyésztési program fajtáira (Pannon Ka, Pannon nagytestű és Pannon fehér) vizsgáltam a mitokondriális DNS D-loop, illetve a citoplazmatikus hatások jelentőségét az alomnagysággal kapcsolatos tulajdonságokra nézve. Ezt a vizsgálatot nyúltenyésztésben eddig még nem alkalmazták. A mitokondriális DNS D-loop, illetve a citoplazmatikus hatások a vizsgált tulajdonságokat érdemben nem befolyásolták. A kapott eredmények hátterében a mitokondriális DNS D-loop csekély variabilitása állhat.

Az élve (NBA), holtan (NBD), illetve összesen (TNB) született fiókák számának genetikai paramétereinek, valamint genetikai trendjeinek becsléséhez az egyes fajtáknál (Pannon nagytestű, Pannon fehér és Pannon Ka) sorrendben 6269 (1469 anya), 21060 (4926 anya), 15833 (3691 anya) fialási rekordot elemeztem, melyet az egyes fajtáknál 1992-2016, 2004-2015 és 1999-2016 között gyűjtöttek a Kaposvári Egyetem Kísérleti Nyúltelepén.

REML eljárást alkalmazva az egyes fajták vizsgált tulajdonságait 12 egytulajdonságos egyedmodellel értékeltem. A becsült öröklődhetőség értéke minden fajtában és tulajdonságban csekély (Pannon nagytestű: NBA: 0,07-0,08± 0,018-0,021; NBD: 0,01-0,02± 0,009; TNB: 0,04-0,05± 0,015-0,018; Pannon fehér: NBA: 0,06-0,07±0,01; NBD: 0,019-0,020±0,003-0,004; TNB: 0,07±0,01; Pannon Ka: 0,07-0,09±0,01; NBD: 0,03±0,01; TNB: 0,07-0,10±0,0) volt.

A becsült tartós környezeti hatások nagysága (a fenotípusos variancia arányában) meghaladta (Pannon nagytestű: NBA: 0,11-0,16± 0,016-0,018; NBD: 0,06-0,07± 0,014-0,015; TNB: 0,11-0,17± 0,014-0,017; Pannon fehér: NBA: 0,07-0,09±0,01; NBD: 0,06-0,07±0,008-0,013; TNB: 0,07-0,10±0,01; Pannon Ka: 0,07-0,11±0,01; NBD: 0,02-0,03±0,01; TNB: 0,07-0,11±0,0) az öröklődhetőségi értékeket.

A modellek illesztésvizsgálata során azt tapasztaltam, hogy az egyes fajták vizsgálati tulajdonságait jellemző modellek nem mutattak torzítottságot. A legjobb modelleket (melyek a fialási sorszámot, az anyai fialáskori életkorát és a fialás év-hónapját tartalmazták) dominanciahatásokkal egészítettem ki.

Ennek következtében a becsölt öröklődhetőségi értékek nagysága (Pannon nagytestű: NBA: 0,06± 0,02; NBD: 0,02-0,012; TNB: 0,02± 0,022; Pannon fehér: NBA: 0,06±0,01; NBD: 0,020±0,01; TNB: 0,06±0,01; Pannon Ka: 0,06±0,01; NBD: 0,02±0,01; TNB: 0,06±0,80) általában csökkent.

A becsült tartós környezeti hatások nagysága (a fenotípusos variancia arányában) szintén csökkent (Pannon nagytestű: NBA: 0,09±0,031; NBD: 0,05± 0,024; TNB: 0,07±0,028; Pannon fehér: NBA: 0,08±0,01; NBD: 0,008±0,005; TNB: 0,08±0,001; Pannon Ka: 0,08±0,01; NBD: 0,01±0,01; TNB: 0,09±0,87).

A dominanciahatások nagysága (a fenotípusos variancia arányában) általában meghaladta a becsült öröklődhetőségi értékek nagyságát (Pannon nagytestű: NBA: 0,27±0,024; NBD: 0,05±0,013; TNB: 0,38±0,025; Pannon fehér: NBA: 0,09±0,01; TNB: 0,16±0,01; Pannon Ka: NBA: 0,16±0,01; NBD: 0,10±0,01; TNB: 0,15±0,69).

A kivétel a Pannon fehér fajtában regisztrált holtan született fiókák száma volt, ahol a kapott értékek elmaradtak (0,01±0,002) a becsült h^2 értékektől.

A dominanciahatásokkal kiegészített egyedmodellek alapján (a modellben szereplő random hatások közti hatáskeveredés miatt) valamivel kisebb genetikai trendeket becsültem a dominanciahatásokat nem tartalmazó modellek alkalmazása esetén kapott eredményekhez viszonyítva (Pannon nagytestű: NBA: 0,035 vs 0,03; NBD: -0,0017 vs -0,003; TNB: 0,016 vs 0,01; Pannon fehér: NBA: 0,027 vs 0,026; NBD: 0,0003 vs -0.0004; TNB: 0,0258 vs 0,0255; Pannon Ka: NBA: 0.05 vs 0.06; NBD: -0,001 vs -0,0016 TNB: 0,06 vs 0,07).

A dominanciát tartalmazó, illetve azt nem tartalmazó egyedmodellek alapján becsült tenyészértékek között minden fajtában és tulajdonságban igen szoros (Pannon nagytestű: 0,96-0,98; Pannon fehér: 0,99; Pannon Ka: 0,98-0,99) rangkorrelációt tapasztaltam.

A dominanciahatások modellbe történő illesztése a legnagyobb tenyészértékű nyulak rangsorát ennek ellenére kis mértékben módosította.

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13. Publications on the subject of the dissertation

Papers published in peer-reviewed journals

Nguyen T.N., Nagyné Kiszlinger H. (2016): Dominance effects in domestic populations. Acta Agraria Kaposváriensis, 20: 1-20.

Nguyen T.N., Farkas J., Szendrő Zs., Nagy I. (2017): Genetic evaluation of litter size traits in Pannon Large rabbits. Anim. Sci. Papers and Reports (In Press), 35: 181-192. http://www.ighz.edu.pl/uploaded/FSiBundleContentBlockBundleEntityTranslatableBlockTranslatableFilesElement/filePath/826/str181-192.pdf

Nguyen T.N., Farkas J., Szendrő Zs., Nagy I. (2017): Genetic Evaluation of litter size traits in Pannon White rabbits. Agric. Conspec. Sci., (accepted).

Nguyen T.N., Brajkovic V., Cubric-Curik V., Ristov S., Veir Z., Szendrő Zs., Nagy I., Curik I. (2017): Analysis of the impact of cytoplasmic and mitochondrial inheritance on litter size and carcass in rabbits. World Rabbit Sci., (under review).

Full-length conference papers in proceedings

Nguyen T.N., Farkas J., Matics Zs., Nagy I. (2016): Comparisions of animal models evaluating the litter traits of the pannon large rabbits. 28. Nyultenyesztesi Tudomanyos Nap, Kaposvar, 33-38.

Nguyen T.N., Curik I., Farkas J., Szendrő Zs., Nagy I. (2017): Genetic Evaluation of litter size traits in Pannon Ka rabbits. Animal Science Days, Brandlucken, Austria (under review).

14. Publications not related to the dissertation

Nagyné Kiszlinger H., Nguyen T.N., Farkas J., Kover G., Nagy I. (2015): Genetic parameters and breeding value stability estimated from a joint evalution of purebred and crossbred sows for litter weigh at weaning. Acta Agraria Kaposvariensis, 19: 1-7.

15. Curriculum vitae

Nguyen Thao Nguyen was born on 24th of December in 1986 in Vinh Long, Vietnam. She graduated from high education in 2004. After completing her studies in Cantho University, Can Tho, Vietnam, she received her degree majoring in Veterinary (M.Sc.) in 2014. From 2014 up to now, she is a PhD student of Kaposvar University.

Since 2009 she worked in Cantho University as a researcher related to animal science and had many internships also related to animal science in Institute of Biotechnology (Vietnam Academy of Science and Technology, Vietnam), Gent University (Belgium), Ryazan State Agrotechnological University (Russia) and Zagreb University (Croatia).

16. Abbreviations

BLUP: best linear unbiased prediction

Bp: base pair

BS: population of Brown Swiss

BV: population of Braunvieh

DNA: Deoxyribonucleic acid

F_{Dam}: inbreeding coefficient of dams

F_{Litter}: inbreeding coefficient of litters

LFCM: lifetime production of fat corrected milk

LPL: length of productive life

LWT: 21-d litter weight

MaGelLan: maternal genealogy lineage analyser

mtDNA: mitochondrial deoxyribonucleic acid

NBA: number born alive

NBD: number born death

Nt: nucleotic

OXPHOS: oxidative phosphorylation

PCR: polymerase chain reaction

PK: pannon ka breed

PL: pannon large breed

PW: pannon white breed

REML: restricted maximum likelihood

TNB: total number born

Vs: versus

17. Annex

Description of rabbit (Oryctolagus cuniculus) haplotype sequences presented in Figure.

Accession #	Origin	Haplotype	Reference	Description
AJ293831	France	H6	Bolet et al., 2000.	Domestic Fauve de Bourgogne
AJ293832	Belgium	H7	Bolet et al., 2000.	Domestic Belgian hare
AJ293833	France	H8	Bolet et al., 2000.	Domestic Fauve de Bourgogne
AJ293834	France	H9	Bolet et al., 2000.	Domestic Argente de Champagne
AJ293835	Great Britain	H10	Bolet et al., 2000.	Domestic English
AJ293836	Belgium	H11	Bolet et al., 2000.	Domestic Flemish giant
AJ293837	France	H12	Bolet et al., 2000.	Domestic Fauve de Bourgogne
AJ293838	Hungary	H13	Bolet et al., 2000.	Domestic Hungarian Giant
AJ293839	France	H14	Bolet et al., 2000.	Domestic French Lop
AJ293840	France	H15	Bolet et al., 2000.	Domestic French Lop
AJ293841	France	H16	Bolet et al., 2000.	Domestic French Lop
AJ293843	Austria	H17	Bolet et al., 2000.	Domestic Vienna White
AJ293844	Belgium	H18	Bolet et al., 2000.	Domestic Flemish Giant
U62924	Australia	H4	Fuller et al., 1997..	Wild rabbit
U62925	Australia	H1	Fuller et al., 1997	Wild rabbit
U62926	Australia	H16	Fuller et al., 1997	Wild rabbit
U62927	Australia	H2	Fuller et al., 1997	Wild rabbit
NC_001913	Unknown	H1	Gissi et al., 1998.	Rabbit reference sequence
AF534080	China	H1	Long et al., 2003.	Qixing
AF534081	China	H1	Long et al., 2003	Haerbin White
AF534082	China	H1	Long et al., 2003	Zhenhai thick-hair Angora

AF534083	China	H1	Long et al., 2003	Big ear brown rabbit
AF534085	Belgium	H1	Long et al., 2003	Belgium
AF534092	China	H1	Long et al., 2003	Sichuan White
AF534094	Germany	H1	Long et al., 2003	Rex
AF534095	Germany	H1	Long et al., 2003	Angora
AF534096	Germany	H1	Long et al., 2003	Zika
AF534097	China	H1	Long et al., 2003	Fujian Brown
AF534098	China	H1	Long et al., 2003	Taihang Moutain
AF534099	China	H3	Long et al., 2003	Yufeng Brown
AF534100	Germany	H2	Long et al., 2003	Zika (Germany great line)
AF534101	Germany	H2	Long et al., 2003	Rex
AF534103	China	H4	Long et al., 2003	Zhenhai thick-hair Angora
AF534104	Japan	H1	Long et al., 2003	Japanese White
AF534105	China	H1	Long et al., 2003	Yufeng Brown
AF534107	Germany	H5	Long et al., 2003	Zika
KY977609	Hungary	H1	This study	Pannon Large
KY977634	Hungary	H1	This study	Pannon Ka
KY977665	Hungary	H1	This study	Pannon White
KY977670	Hungary	H2	This study	Pannon White
Z83340	Spain/Portugal	H19	van der Loo et al., 1997	Wild rabbit
Z83341	Spain/Portugal	H20	van der Loo et al., 1997	Wild rabbit
Z83342	Spain/Portugal	H21	van der Loo et al., 1997	Wild rabbit
Z83343	Spain/Portugal	H22	van der Loo et al., 1997	Wild rabbit

Z83344	Spain/Portugal	H23	van der Loo et al., 1997	Wild rabbit
Z83346	Spain	H24	van der Loo et al., 1997	Wild rabbit
Z83347	Spain	H25	van der Loo et al., 1997	Wild rabbit
Z83348	Spain	H26	van der Loo et al., 1997	Wild rabbit
Z83350	Spain	H27	van der Loo et al., 1997	Wild rabbit
Z83352	Spain	H16	van der Loo et al., 1997	Wild rabbit
Z83354	Spain	H28	van der Loo et al., 1997	Wild rabbit
Z83355	Spain	H29	van der Loo et al., 1997	Wild rabbit
Z83356	Spain	H30	van der Loo et al., 1997	Wild rabbit
Z83357	Spain	H31	van der Loo et al., 1997	Wild rabbit
Z83358	Spain	H32	van der Loo et al., 1997	Wild rabbit
Z83359	Spain	H33	van der Loo et al., 1997	Wild rabbit
Z83360	Spain	H34	van der Loo et al., 1997	Wild rabbit
Z83361	Spain	H35	van der Loo et al., 1997	Wild rabbit
Z83362	Spain	H36	van der Loo et al., 1997	Wild rabbit
Z83363	Spain	H37	van der Loo et al., 1997	Wild rabbit
Z83364	Spain	H38	van der Loo et al., 1997	Wild rabbit
Z83365	Spain	H2	van der Loo et al., 1997	Wild rabbit
Z83366	Spain	H4	van der Loo et al., 1997	Wild rabbit
Z83367	Spain	H1	van der Loo et al., 1997	Wild rabbit

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Zagreb, May 11th, 2017

Dr. István Nagy

University of Kaposvár

40 Guba S. str., H-7400 Kaposvár, Hungary

Dear Dr. Nagy

I am glad to inform you that your manuscript No. 1221 entitled "Genetic evaluation of litter size traits in Pannon White rabbits" has been accepted for publication in Agriculturae Conspectus Scientificus as an Original Scientific Paper.

Thank you for your interest in Agriculturae Conspectus Scientificus. I am looking forward to collaborating with you in the future.

Kind regards,

Professor Zlatko Šatović

ACS Editor in Chief

Prof. dr. sc. Zlatko Šatović

ACS Editor in Chief